OSTRACOD PHYLOGENY AND EVOLUTION – THIRTY YEARS AFTER "MANAWAN PERSPECTIVE"

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Abstract. The Recent ostracod species *Manawa staceyi* Swanson, 1989, belonging to the superfamily Puncioidea, was originally considered a relict species related to the Palaeozoic Palaeocopa, ostracods, now extinct. During the last 30 years research on *Manawa* documented the basal position of the superfamily Puncioidea within the phylogenetic tree of the Subclass Podocopa. The Palaeocopa is possibly a heterogenous taxon containing both myodocopids and podocopids. Re-examination of the systematic position, phylogenetic affinities and evolution of the superfamily Puncioidea is presented using information from the comparative analysis of the body plans of Myodocopa and Podocopa, rationalised within morpho-functional modules: the carapace as a 'protective' construct, the ambulatory complex, combined with feeding, reproductive and sensory systems. The significant traits of the different morpho-functional modules of the superfamily Puncioidea when compared to those of the ostracod Orders Podocopida and Platycopida suggest for the former group an independent phylogenetic position within the Subclass Podocopa, taxonomically treated as Order Punciocopida Schallreuter, 1968. Morphological traits such as the maxillulary endopodite and the 8th body limb of *M. staceyi* are considered deep genetic homologies existing within the Subclass Podocopa at the level of cellular regulatory systems. The widely gaping valves held in a 'horizontal' plane during the ambulatory activity and the collaborative structure and position of the 2nd antenna continued with respect to the 5th to 7th pair of limbs are considered solutions (adaptations) to psammobiotic life within the dynamic shallow marine habitats. Examination of the discrepancy between the low species diversity of Puncioidea and those of the species-rich non-marine Cypridoidea may be as a result of the major differences in the way representatives of the two ostracod groups are able to actively perceive the surrounding environment as well as to their capacity to construct their niche, leading to successful speciation.

Key words: Marine Ostracoda, Punciocopida, Body plans, taxonomy, functional morphology, species diversity

1. INTRODUCTION

Ostracoda is one crustacean group noted for its extremely high species diversity. The World Data Base (Brandão *et al.*, 2019) indicates about 50,000 living and fossil species. Ostracods display also a bright spectrum of disparity patterns (see *inter alia*, the monographic treatment of Hartmann, 1966 – 1989). There are records of Palaeozoic (Ordovician) of several supposed ostracod groups (Siveter, 2008; Williams *et al.*, 2008). The only ostracods with soft-parts found, occur in a myodocope from the Upper Ordovician (Siveter *et al.*, 2014). When compared to other Crustacea groups, for example the Malacostraca, ostracods display an excellent and relatively-complete fossil record (Foote and Sepkosky, 1999). As a result, ostracod taxa possessing both fossil and living representatives have proved useful subject for phylogenetic reconstructions. One such group is the superfamily Puncioidea (Hornibrook, 1949) with representatives known from the Upper Triassic to present-day (Hornibrook, 1949; Swanson, 1991; Kozur, 1998), and with affinities to the Palaeocopa Henningsmoen, 1953, an ostracod group which flourished during the Palaeozoic but became extinct at the end of that epoch or during the early Mesozoic (Swanson, 1991; Becker and Swanson, 1992; Kozur, 1998).

In 1949, Hornibrook described two monotypic genera *Puncia* and *Manawa* for which he proposed the new family Punciidae. The two new ostracod taxa were being represented only by empty valves; one, a juvenile belonging to the new species *Puncia novozealandica* Hornibrook (Fig. 1 a-b) and four other valves identified by Hornibrook (1949) as *Manawa triphaena* Hornibrook (Fig. 1 c-e). They resembled the palaeocopid ostracod *Eurichilina reticulata* Ulrich (Fig. 1f).

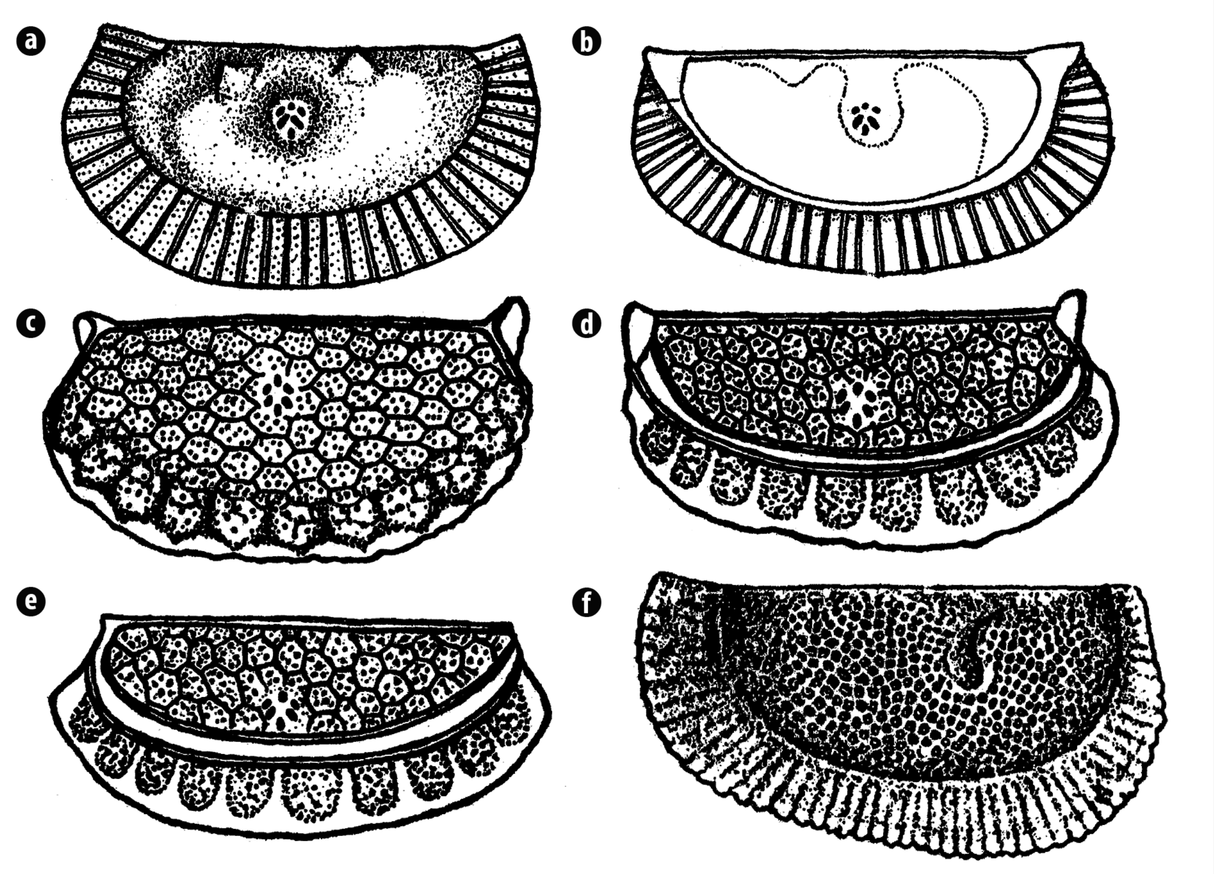


Figure 1. a-e – Ostracoda Punciidae resembling Palaeozoic Beyrichidae: **a,b** – *Puncia novozealandica*, LV; **a** – E-side; **b** – I-side; **c-e** – *Manawa triphena*; **c,d** – RV; **c** – E-side; **d** – I-side; **e** – LV I-side; **f** – *Eurichilina reticulata*, RVE. (from Hornibrook, 1949)

Hornibrook's material was isolated from Recent sediment dredged from the Three Kings area, off Northland, New Zealand, at depths of between 140 m and 180 m (Hornibrook, 1949). In (1985) Swanson then made the first successful recovery of living specimens of *Manawa*, these collected from the benthos at littoral depths on the north-eastern coast of North Island, New Zealand. This discovery then lead to detailed descriptions of both the limb morphology and aspects of the animal behaviour.

During the 1st European Ostracod Meeting (EOM), held at Senckenberg Institute and Museum, in Frankfurt/Main, August 1989, Kerry Swanson delivered a challenging lecture titled, "Ostracod phylogeny and evolution – a manawan perspective" (Swanson, 1989a). In that presentation the implications of observations made on living specimens of *Manawa* for phylogenetic reconstructions of different ostracod groups, especially Palaeozoic taxa such as the palaeocope Kirkbyoidea (for which only valve morphologies are described) were discussed. Swanson (1989a) illustrated and highlighted several novelties of *Manawa* such as its widely-gaping valves (Fig. 2a) when moving and, the presence of a special valve structure he named "stragular process" (Fig. 2b). Additionally, it was emphasised (Swanson, 1990) that the limb morphology and the peculiar postembryonal development of *Manawa* could help to better fix the position of Ostracoda within the crustacean Maxillopoda (Newman, 2005).

During the EOM event Swanson presented also morphologic details on a new species, *Manawa staceyi* (Swanson 1989b). This latter was considered by Malz (1990) an example of relict species, a so-called "living fossil", belonging to an ostracod group largely extinct during the Mesozoic and Cenozoic eras (Fig. 3).

Inevitably, after Swanson's presentation of the "manawan perspective", new contributions dealing with the phylogeny and evolution of the ostracods belonging to the superfamily Puncioidea were published. Becker and Swanson (1992) considered that this group represents a primitive palaeocopid group but their opinions diverged, especially in relation to a possible affiliation to the Palaeozoic Kirkbyocopina.

Results of a cladistical analysis, using morphologic traits of both valves and limbs was later presented by Horne *et al.* (2005). The Punciodea was considered to belong to the Order Kirkbyocopina, with the latter appearing as a member of the Subclass Podocopa. The puncioids on the cladogram of Horne *et al.* (2005) had a basal position, as they were first derived from the main stock of the podocopans. Oakley *et al.* (2012) in their cladistic analysis using information from the molecular data of mitochondrial genome, nuclear genome, and ribosomal DNA of a large set of ostracod taxa, (including *Manawa staceyi*) reached a conclusion that very much paralleled that of Horne *et al.* (2005). Also of relevance with respect to the present discussion are the results of Tinn and Oakley (2008). Based on molecular-clock algorithms, their calculations indicated that the separation of *Manawa staceyi* from its closest Puncioidea relatives probably occurred about 500 Mya ago. Those authors also concluding that change in Puncioidea reflected a very low evolutionary rate. Summing up these results, it might then be proposed that *Manawa staceyi* is the living relict of an extremely old, primitive ostracod group.

In the following discussion, the authors wish to highlight why the “manawan perspective” continues to fascinate, especially when this is then placed within the context of recent progress made in evolutionary biology and modern ostracod systematics. More precisely our project deals with a re-evaluation of the morphological traits of *Manawa staceyi* in order to challenge the paradigmatic view of the primitive state of this species. We will also try to more appropriately fix the evolutionary position of the superfamily Puncioidea on the traditional phylogenetic scheme published by G. W. Müller (1894). Figure 4 presented herein being an adapted version of Müller’s original scheme; and is considered useful for the discussion surrounding the various opinions on the systematic position of the superfamily Puncioidea within the class of Ostracoda.

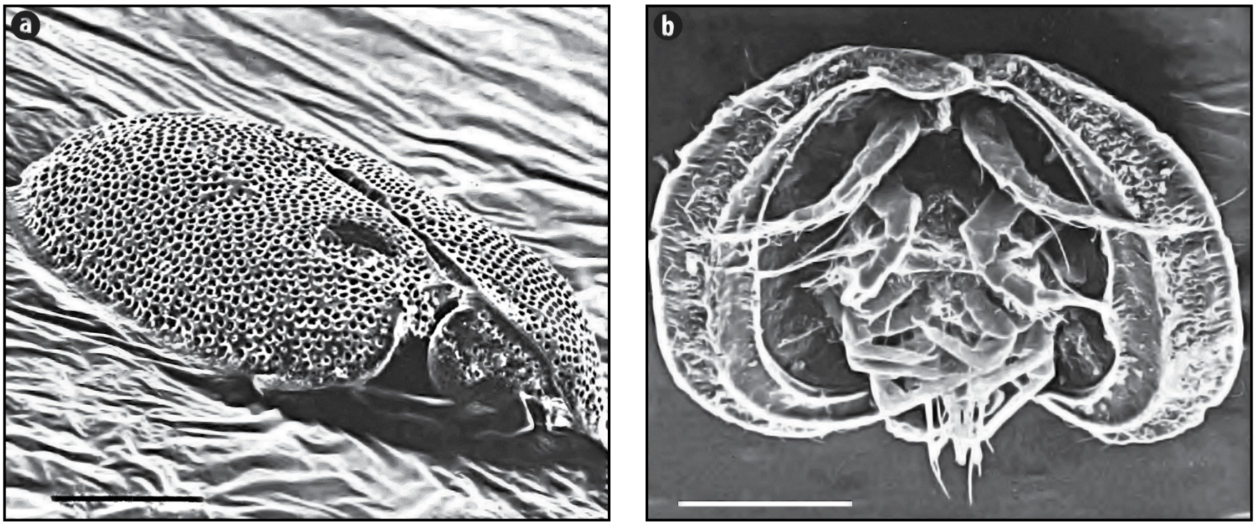
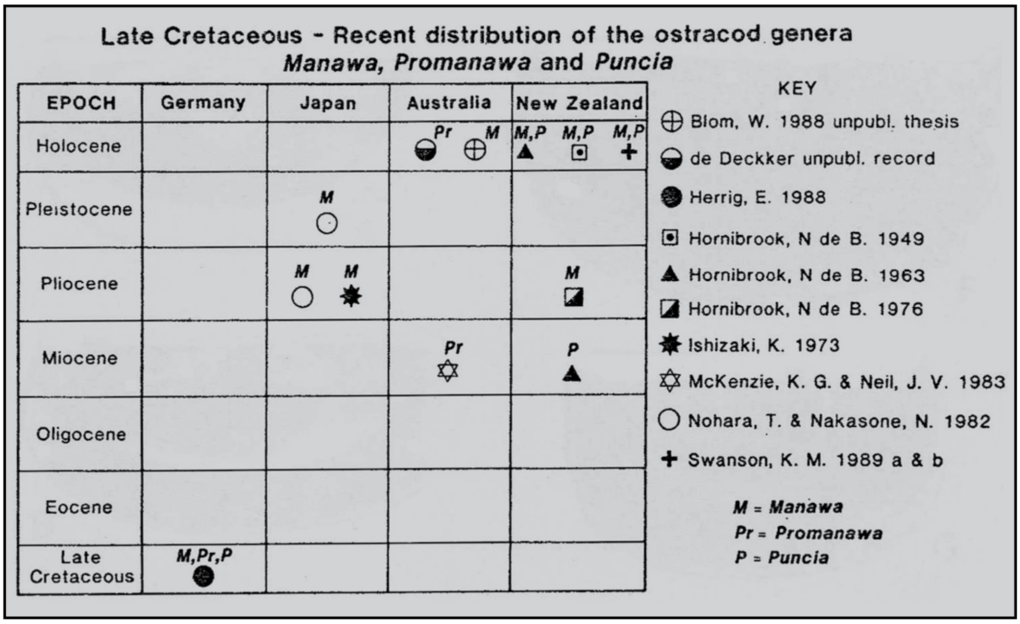


Figure 2. a-b – *Manawa staceyi* Swanson: **a** – E-side,valves with bright gape; **b-c** – I-side, RV with anterior “stragular process” (scale bars = 0.1mm) (from Swanson, 1989a).



Late Cretaceous - Recent distribution of the ostracod genera
Manawa, Promanawa and *Puncia*

EPOCH	Germany	Japan	Australia	New Zealand
Holocene			Pr ◒ M ⊕	M,P ▲ M,P ⊡ M,P ✚
Pleistocene		M ○		
Pliocene		M ○ M ✸		M ◪
Miocene			Pr ✡	P ▲
Oligocene				
Eocene				
Late Cretaceous	M,Pr,P ●			

KEY
⊕ Blom, W. 1988 unpubl. thesis
◒ de Deckker unpubl. record
● Herrig, E. 1988
⊡ Hornibrook, N de B. 1949
▲ Hornibrook, N de B. 1963
◪ Hornibrook, N de B. 1976
✸ Ishizaki, K. 1973
✡ McKenzie, K. G. & Neil, J. V. 1983
○ Nohara, T. & Nakasone, N. 1982
✚ Swanson, K. M. 1989 a & b

M = *Manawa*
Pr = *Promanawa*
P = *Puncia*

Figure 3. Spatio-temporal distribution of the Punciidae taxa, as known in 1990 (from Swanson, 1991).

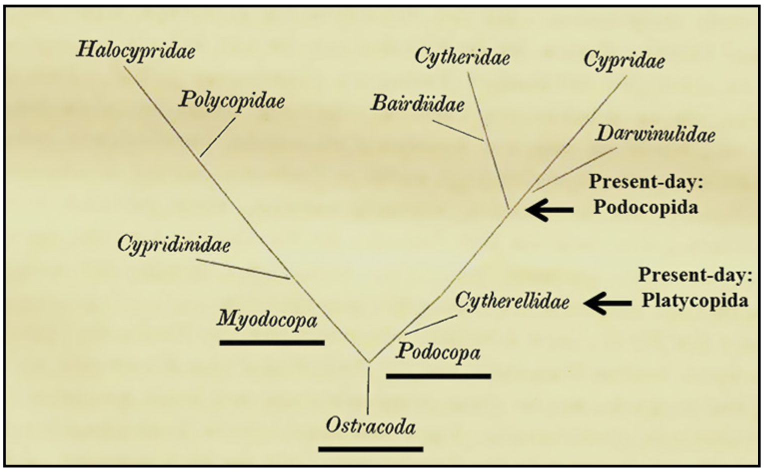


Figure 4. Phylogenetic tree representing Recent Ostracoda taxa (from G.W. Müller, 1894, adapted to the taxonomic scheme of Martin and Davis, 2001).

Table 1. Taxonomic position of the members of superfamily Puncioidea Hornibrook within different Crustacea Subclasses and Orders.

Taxonomic hierarchy	Proposed Taxonomic Position	Authority
Subclass Palaeocopa [*]	Order Beyrichicopida [**]	Henningsmoen 1953
Subclass Palaeocopa	Order Beyrichicopida	Sylvester-Bradley 1961 [***]
Subclass Palaeocopa	Order Palaeocopida [1]	Swanson 1991; Becker & Swanson 1992
Subclass Palaeocopa [2]	No order assignment	Abushik 2015
Subclass Palaeocopa	No order assignment	Brandão et al. 2019
Subclass Platycopa [3]	Order Punciocopida [4]	Schallreuter 1968; Hinz-Schallreuter & Schallreuter 1999
Subclass Podocopa	Order Palaeocopida	Horne 2003; Horne & al. 2002, 2005; Oakley & al. 2012
Subclass Podocopa	Order Platycopida [5]	Martin & Davis 2001
Subclass Podocopa	Order Podocopida	Ishizaki 1973; McKenzie &Neil 1983
Subclass Podocopa [6]	Order Punciocopida	Liebau 2005
Subclass Podocopa	Uncertain assignment to Podocopa	Cohen & al. 1998
Subclass Punciocopa	New Subclass	Yu Na & al. 2012

Notes: [*] originally described by Henningsmoen 1953 as suborder; [**] Uncertain assignment to Beyrichicopida (= Superfam. Beyrichiacea) in Hennigsmoen 1953, p.235; [***] Sylvester-Bradley,1961, p. 178, superfamily uncertain; [1] Palaeocopina in Becker 1990, p. 159; Becker & Swanson 1992, p. 124; [2] – palaeocopid *sensu lato*, also palaeocopamorph, in Abushik 2015, p. 489; [3] in Martin & Davis 2001, Platycopa is treated as Order of the Subclass Podocopa (see below); [4] Punciocopida is treated as suborder in Schallreuter 1968, p. 150 and in Hinz-Schallreuter & Schallreuter1999, p.121; [5] following a suggestion of R. Whatley which does not exist in Whatley & al.1993, also mentioned as Incertae Sedis; [6] mentioned as Superorder Podocopomorpha, in Liebau 2005, p. 120.

Table 1 summarises that wide range of opinion related to that taxonomical position within various systematic schemes of Ostracoda. In this text, it is our intention to review this taxonomical aspect, using additional and/or alternative observations and viewpoints. In this way we hope to offer a more robust solution to resistant problems that have remained within Puncioidea systematics.

The 'problem' of the bradythelic evolutionary-rate displayed by *Manawa staceyi* mentioned above will be incorporated into a broader discussion of low species diversity in the context of all Puncioidea as compared to the non-marine podocopids. We will propose an explanatory model for the rarity of puncioids, based on observations related to their morphology and ecology. To that end, we will focus attention on observations we have for *Manawa staceyi,* combined with ideas derived from the theory of niche construction (Lewontin, 1985; Odling-Smee *et al.*, 2003).

2. MATERIAL AND METHODS

2.1. INFORMATION ON THE OSTRACOD MATERIAL

Puncioidea ostracods have remained an elusive target since interest was first peaked by Hornibrook (1949). Until 1983, only empty valves were recovered, the vast majority of these from New Zealand, Japan and Australia (Swanson, 1985). Table 2 presents a synoptic view with information for all the known species.

For the material discussed herein the following abbreviations are used: V = Valve; LV = Left Valve; RV = Right Valve; C=Carapace; m=adult male; f=adult female; j=juvenile; E = External side; I = internal side; Recent = live specimens; A1-antennule; A2-second antenna; M-Metanauplius; Md-mandible; Mxl-maxillule; L – body appendage, used for thoracic limbs; Fu –furca; Pe – hemipenis; StPC – Sieve type Pore Canal.

Table 2. Taxa of the Superfamily Puncioidea Hornibrook 1949

Taxon	Author, year	Site	Geographic area	Origin (R/F)	Material
F. Punciidae	Hornibrook, 1949				
Puncia	Hornibrook, 1949				
P. novozealandica	Hornibrook, 1949	N-Cap area	New Zealand	R	AV-1; JV-1
P. goodwoodensis	Hornibrook, 1963	N-Dunedin	New Zealand	F: L-Miocene	AV-1
P. laevis	Herrig, 1988	Isl. Rügen	N-Germany	F: U-Cretaceous	AV-1; JV-1
P. nodosa	Herrig, 1991	Greifswald-area	N-Germany	F: U-Cretaceous	AV-1
Manawa	Hornibrook, 1949				
M. triphena	Hornibrook, 1949	N-Cap area	New Zealand	R	AV-2
M. staceyi	Swanson, 1985, 1989	Goat Island	New Zealand	R	** (A&J) - n
_Manawa sp._*	Blom 1988		Australia	F: Pleistocene	Not known.
M. supracretacea	Herrig, 1988	Isl. Rügen	N-Germany	F: U-Cretaceous	AV-2; JV-1
Promanawa	McKenzie & Neil, 1983				
Pr. australiensis	McKenzie & Neil, 1983	Hamilton, Victoria	Australia	F: L-M Miocene	AV-1
Pr. konishii	Nohara, 1976	Okinawa-Jima	Japan	R, F: Pliocene	***a–A - n; b AV-1
Promanawa sp.	De Deckker unpubl.	Macquarie Harbour	Tasmania	R	Not known
Pr. exposita	Herrig, 1988	Isl. Rügen	N-Germany	F: U-Cretaceous	AV-3; JV-2
F. Triassopunciidae	Kozur, 1998				
Triassopuncia	Kozur, 1998				
Tr. schallreuteri	Kozur, 1998	Silickà Brezová	Slovakia	U-Triass	V-4
Tr. norica	Kozur, 1998	Silickà Brezová	Slovakia	U-Triass	V-1
Triassomanawa	Kozur, 1998				
Tr. lobata	Kozur, 1998	Silickà Brezová	Slovakia	U-Triass	V-1
Tr. reticulostriata	Kozur, 1998	Silickà Brezová	Slovakia	U-Triass	V-1

Note: R – Recent (living) or Holocene; F – fossil, older as Holocene; N – North; L – Lower; U – Upper; M-Middle; * mentioned by Swanson, 1991, p.78 (DLD – presumably new species?). N° – 1,2, 3…n – numbers of individual items, more than 10 individuals; V – valve; A-adult; J-Juvenile; ** see text; *** (a) Hanai & Tabuki, 1995, (b) Iwatani, Irizuki & Yasuhara, 2013.

The analysis and discussion presented below is based mainly on specimens of *Manawa staceyi* collected by one of us (KMS) from the Cavalli Islands at 13 m and 17 m depths off Northland, New Zealand and from the marine reserve at Goat Island (Auckland, New Zealand) at a depth of 17 m (Swanson, 1989b).

The recovery of living specimens of *Manawa* has proved an extremely demanding objective. Specimens were collected using a hand-held dredge which allowed Scuba divers to skim the top 40 mm of the sea-floor sediment at the above mentioned depths. Off Goat Island (the type locality of *M. staceyi*), the see-floor in the target area is a "megaripple zone" with shelly, moderately sorted coarse sand (Swanson, 1989b). The total sediment haul for each sampling period, (two days of work), was approximately 20 litres of sandy sediment. That volume is simply a reflection of the strength of currents operating in the water column of the study area. From the initial raw sediment sample, about 500 ml of fines/organic material was concentrated by using a bulk stir, settle and decant process. Resultant, unwanted coarse sediment residues then being returned to the sampling site. Preserved concentrates were then returned to the laboratory where a search for live manawan specimens was undertaken using a stereo-microscope. One such sampling period resulted in the recovery of only 13 specimens; a return rate of one specimen per three hours of microscope time.

A few of the specimens were deposited in the catalogued collection of NIWA (National Institute of Water and Atmospheric Science), additional specimens were also lodged in the collection of GNS (Geological and Nuclear Sciences). It should also be noted that because of their novelty and the scientific interest in punciid ostracods, one of us (KMS) spent considerable time experimenting with the development of laboratory procedures to prepare specimens for electron microscopy especially. With respect to transmission electron microscopy (TEM), the intention was to develop a technique that would allow vertical, serial-sectioning of oriented specimens such that the microtome knife cut both soft anatomy and the carapace. This is an indication of the importance placed on the 'adductorial' muscle connections between the animal and the gaping valves. This effort resulting in a single successful section which was subsequently lost as a result of destruction by the electron beam (too high current?). This comment is simply an indication as to why so few specimens have been able to be lodged in catalogued collections.

2.2. METHODOLOGICAL TREATMENT

Brief information on the selected approaches we use for the arguments presented in the essay is presented.

2.2.1. Ostracod taxa as units of evolution and units of classification

The long and fraught debate about how to treat species, and by extension other taxonomic units, are they to be considered as evolutionary lineages (*inter alia* Racovitza, 1926; de Queiroz, 1999) or just as a type of historical nominalism (Ereshefsky, 1989). Dupré (2001) offered one solution, namely that taxa (Dupré refers especially to species) have to be viewed both, as units of evolutionary lineages (these latter driven by organismic and environmental processes) and, as units of classification (derived from the decisions of expert taxonomists). Emil G. Racovitza repeatedly noted that taxonomy has to reflect the history of phylogenetic lineages (for a review of that author's views, see Tabacaru et al, 2018). In our discussion, we will follow that train of thought, in the sense that we consider this can be achieved by extraction of information embedded within the organism's quasi-independent morphological and functional characters using same to reach decisions on the selected taxonomy of phylogenetic lineages.

The interest of the approach we favour will become apparent in the context of the way we treat in this essay the Subclasses Podocopa Sars, 1866 and Palaeocopa Henningsmoen, 1953; the validity of the latter being more recently questioned by Siveter *et al.* (2012). Within the discussion on the puncioids we will offer additional arguments which strengthen Siveter's views.

2.2.2. The body plan approach

The 'Body plan' is a concept which was repeatedly criticised as a result of its idealistic connotation (see for instance its usage in Jeannel (1950), and associated arguments related to orthogenetic evolution) but which has been resurrected in the modern biological literature, especially that related to evolutionary developmental (Evo-Devo) research. In the present text, we view body plans as distinctive ensembles of persistent biological traits "of homologous architectural and structural features" as defined by Valentine (1985). Body plans build a type of profile which characterises taxa of higher level within the systematic hierarchy. In the case of the present ostracod project we will use it at the level of Subclasses and Orders Complementary discussion for the body plans have been presented by Arthur (1997) and/or Wagner and Laubichler (2004). Body plans reflect also adaptive solutions to specific kinds of environment. Schram (2013) noted that the high disparity of body plans existing within the subphylum Crustacea is a reflection of their huge range of adaptive solutions to the environmental possibilities. Having this in mind, Schram (op. cit.) questioned the view that Crustacea is a monophylum. This dilemma possibly applies also to the class of Ostracoda where Wakayama (2007) considered that the differences existing between the embryonic developmental patterns of Myodocopa and Podocopa indicate a polyphyletic origin of this crustacean class. However, Oakley and co-workers (2012) have resolved a monophyletic origin for the Ostracoda, to which we subscribe considering morphologic arguments.

Here we will follow Vannier and Abe (1995) who discriminated two body plans within the Ostracoda. Body Plan 1 is characterised by morphologic traits which present a prominent frontal polarity, one that is well adapted for life in oceanic waters (this is the case of representatives of the Subclass Myodocopa). Body Plan 2 displays predominantly ventral polarity, as in the case of Podocopa ostracods, a group which is predominantly benthic in habit. More information on these two body plans, is presented in the Results section of this essay (useful with respect to comparative morphological arguments surrounding the taxonomic position of the superfamily Puncioidea within the class of Ostracoda).

The body plan approach adopted herein is an alternative view to the phylogenetic representation, as used by Horne *et al.* (2005). Our colleagues derived their taxonomic model from cladistical analyses of character states using taxic homologies. In other words, they looked for synapomorphic traits derived from ancestral taxa. In comparison to this "tree thinking" approach (O'Hara, 1997), our definition of body plan is inspired by what Wagner (2016) termed "homology thinking". It uses *inter alia* information on what is now called deep homologies (discussed below).

2.2.3. The Deep Homology concept

Deep Homology is a term proposed by Shubin *et al.* (1997) for morphogenetic processes which act by molecular genetic mechanisms that are homologous and deeply conserved across a wide range of taxa. The conceptual approach was further developed by Shubin at al. (2009) to explain particular morphologies which display approximate similarities and historical continuity at the level of the phenotype but do not fulfil criteria of classic homologies. In the words of these authors "Deep homology … lies in the complex regulatory circuitry inherited from a common ancestor" (Shubin at al., 2009, p.818). The major interest in deep homology patterns is as a result of their potential to explain two morphological processes. In the first instance they account for the appearance of traits considered morphologic novelties. Additionally, they then also explain morphologic similarities due to parallel evolution (Wagner, 2014). It is in this context that particular aspects of morphological similarities existing between various podocope ostracod groups, but lacking a close phylogenetic relationship will be discussed.

2.2.4. Morphological characters as structural and functional modules

Any organism may be differentiated into it component parts and these then assembled into structural modules, each with a different degree of complexity. Modules in the modern evolutionary biological literature (*inter alia* Wagner *et al.*, 2007) are defined as an integrated assemblage of structures displaying network interactions. A modular unit is composed by subunits which in a general sense, are quasi-independent (i.e. relatively autonomous) structures (Lewontin 2001).

Considering the podocopid ostracods, Danielopol and Martens (*in* Danielopol *et al.*, 1989, p. 88) attempted to introduce and popularise the modularity principle amongst ostracodolgists and related disciplines. In that publication the authors made the following observations about the cytheroid ostracod *Leucocythere mirabilis* Kaufmann: "The morphology of an organism can be viewed through a functional analysis of the various character states. We can classify the morphological characters of an ostracod in several groups or modules. For example most of morphological characters of the carapace cooperate for one main function: the protection of the soft body structure. The main parts of the A2 and of the walking limbs cooperate as one module to the locomotory function. The sensorial setae of the A1 and A2 and parts of the thoracic legs (especially the third walking limb) as well as the furca and the copulatory appendages participate in the mating process. For the feeding function, we have a module represented by the antennae (parts of their structure), the mandible, the maxillula, and partly the first walking limb (maxilla?). Parts of some of the limbs, for instance the distal endopodial podomeres of the antennae, are involved in several functional modules at once: in this case the locomotion, the feeding and the mating."

The pioneering work on the functional modular complex of one group ostracods (deposit feeding complex of *Cypridopsis vidua* (O.F. Müller) by Graham Cannon (1926) must be acknowledged. More recently, Horne *et al.* (1998) presented details on the copulatory module involved in the matting process exhibited by a number of ostracod groups.

Finally, it must be noted that structural and functional modules, as used herein, represent the building blocks of the body plans under study. Morphologic modules integrate also aspects of historical and ecological context within which organisms develop and further as phylogenetic lineages evolve (Klingenberg, 2008).

2.2.5. The Niche Construction Theory

With regards to evolutionary ecology, in 1957, G. E. Hutchinson promoted the description of the ecological properties of species by using the way they react to the environment they experience. This is a "realized niche" but is theoretically something that can also be visualised within a multidimensional hyperspace.

More recently, a strong debate developed around the necessity to insert within evolutionary studies, more information about the organism-environment relationship, in order to expand the Modern Synthesis thinking (*inter alia* Laland *et al.*, 2014). Richard Lewontin (*cf.* Lewontin, 1985) made compelling arguments highlighting the necessity to treat organisms as subjects and objects of selection processes. That author then indicating that living organisms perceive actively the environment and are able to actively explore and to use or change the environment where they live. In other words, organisms are able to construct their environment which then impacts on the long-term organismic evolution of a given species.

Odling-Smee *et al.* (2003), in their book "Niche construction; the neglected process in evolution", further developed and formalised these ideas into the so-called Niche Construction Theory (NCT). Supporters of this conceptual model indicating that researchers must pay more attention to the processes which lead to the reciprocal coevolution of organisms and their environments. The NCT places more emphasis on the dynamic complexity of the organism-environment relationships at different spatial scales. With respect to the present discussion, NCT offers support for viewing the development and/or the maintenance of species diversity as a consequence of the perceptual capacities of species, within their exploration activity and the subsequent selection of habitats which best fit their biological requirements. Within this context, the opinion of Rosenzweig (1987) is of interest, he suggested that one of the causes for the origin of high species diversity in spatial heterogenous environments is the active habitat investigation by individuals searching for spaces that meet their biological requirements.

The active exploration of selected habitats has also been described by one of us (DLD) in a number of publications, these including observations on the active selection of a habitats by groundwater dwelling isopods under natural conditions in the field (Rouch and Danielopol, e 1999), and lacustrine ostracods observed in controlled laboratory conditions (Danielopol *et al.*, 1990; Roca and Danielopol, 1991). Additionally, a case study dealing with the behaviour of a candonid and a cypridoid (Danielopol *et al.*, 2019) will be presented later in this text. This approach is important in order to get a comparative view with respect to our explanatory model for the rarity of Puncioidea diversity.

2.2.6. Notes on the classificatory system of Ostracoda used

Myodocopa and Podocopa as taxonomic units and their diagnostic definitions were proposed originally by G.O. Sars (1866), and later emended by G.W. Müller (1894). In the current text, these are used within the framework of the updated classificatory system of Crustacea devised by Martin and Davis (2001). Their taxonomic hierarchy is the result of the synthesis of a huge amount of information including the entire spectrum of diverse body limbs exhibited by that subphylum. The Martin and Davis (2001) system, used largely also by Horne *et al.* (2002), considers Myodocopa and Podocopa Subclasses belonging to the class Ostracoda. It does not consider taxonomic units related to exclusively fossil ostracods, in this regard refer to Whatley *et al.* (1993) and/or Becker and Braun (2007). Note that here, following the critical observation of Becker (in Becker and Braun, 2007) we will not use the taxonomic units proposed by Kozur (1972, 1993) and partly followed by Liebau (2005).

Gunnar Henningsmoen (1953, p. 188) proposed the Suborder Palaeocopa , equivalent to the Suborder Podocopa. The original diagnosis of that new subororder was: "Shell without frontal opening. Hinge line straight and usually long. Apparently, no calcareous inner lamella. There is a tendency to develop lobes and sulci, and submarginal ridges. Animal unknown". Brandão *et al.* (2019) used the Henningsmoen taxon as a Subclass, Palaeocopa, while Horne *et al.* (2002) considered it an order within the Subclass Podocopa.

Swanson (1991) proposed to link the superfamily Puncioidea with the Palaeozoic ostracod group Kirkbyoidea and then combine these within the Palaeocopa. This latter is considered a Suborder, Kirkbyocopina, in Horne *et al.* (2002) and the superfamily Puncioidea is a member of Kirkbyocopina.

3. RESULTS

3.1. Body plans of Myodocopa G.O. Sars, 1866. emend. G.W. Müller, 1894 and Podocopa G.O. Sars, 1866.

These two body plans are herein defined mainly by characteristics of the limbs and less by those of the carapace (Table 3).

The morphologic profile of Myodocopa, named Body plan 1 by Vannier and Abe (1995), has as a general characteristic its so-called frontal polarity. As a group, these ostracods advance in water mainly by swimming using strong antennae. The basipodite of the A2 especially, is very muscular and the exopodite is long with many podomeres. The valves of the swimming myodocopes have generally a convex ventral margin and low asymmetry. The sensorial organs, have a predominantly frontal position. This is the case for the Belonci organ and aestetascs on the antennule. Ocular organs are represented by two different types , a naupliar eye and lateral ocular organs. The male clasping organs are represented by structures on the endopodite of the antenna. The thoracic limbs L5 and L6 display phylopodial structures. The maxillule lacks a branchial plate. The position of the furca is posterior to the anus. In some groups, the circulatory system involves the entire body. Finally embryonal development begins with two embryonal buds (Wakayama, 2007).

The morphologic profile of the Podocopa, Body plan 2, displays a ventral polarity. This means that those ostracods advance mainly on the bottom of or within the substrate by crawling. The valves have generally a straight or slightly concave ventral margin. The right and left valves of many species are asymmetric. Ambulatory limbs have a ventral position and are commonly used for crawling. The basipodite of the A2 (Fig. 6) is elongated and does not display strong muscular development as is the case for Myodocopa. The endopodite of the antenna is well developed with maximal four podomeres, while the exopodite is reduced to one or two podomeres. The male clasping organ is represented by transformed endopodial podomeres of the thoracic limbs. The L5 and L6 display stenopodial endopodites.

The sensorial organs are mainly developed on the endopdite of the 2nd antenna and the ocular organ is represented by a naupliar eye. The maxillule has a respiratory plate (exopodite). The position of the furca is anterior to the anus. No circulatory organs exist and the embryonal development proceeds by the splitting of one embryonal bud (Wakayama, 2007).

3.2. Deep homologies of Puncioidea

3.2.1. The maxillular endopodite of M. staceyi

The 4th limb of *Manawa staceyi* is the maxillula (termed maxilla in Swanson 1989b). Figure 7a shows the general structure of the female limb with a distal endite as "masticatory process" and a pediform palp. This latter is interpreted as an endopodite with the typical podomeres, ischium, merus, carpus, propodus and dactylus. For comparative purpose we present (Fig.14) the structure of the maxillula and the 5th to 7 limbs existing on the podocopan bairdiid *Anchistrocheles angulata* (Brady). In the latter case, the maxillula presents three distal masticatory endites and the pediform endopodite occurs on the thoracic limbs. The 5th limb in the case of podocopan cypridoids also displays reduced endopodites (Fig. 7 i-k), thus resembling that of *M. staceyi*.

The male's endopodite of the maxillula is in *M. staceyi* transformed into a clasping organ (Fig. 7b-c). Because of the transformed endopodite, this resembles the 5th limb of the podocopan cypridoids (Fig. 7f-g). In this latter case, we note a trend of reduction from an endopodite with several podomeres (with an ischium and merus, a fused carpus with the propodus and a minute dactylus) as in the case of Ilyocypridae (Fig. 7f) to those of the Candonidae where the endopodite is represented by only one, strongly sclerified segment, (Fig. 7h). The platycopid *Cytherella sordida* displays transformed endopodites in a clasping organ on both 5th and 6th limbs. These examples show a parallel evolution of the endopodite structure of thoracic limbs (Fig. 7d-e).

3.2.2. The 8th limb of M. staceyi

Swanson (1989b, p. 239) described the 8th limb as an assumed uropod. This is also figured in Horne *et al.* (2002, p. 14). Here we compare the 8th limb of *Manawa staceyi* (Fig. 8a) with the brush like organ of *Cytherella sordida* Sars (Fig. 8b), illustrated by G.W. Müller (1894) and reproduced by Hartmann (1966, p. 214). Following the latter author,

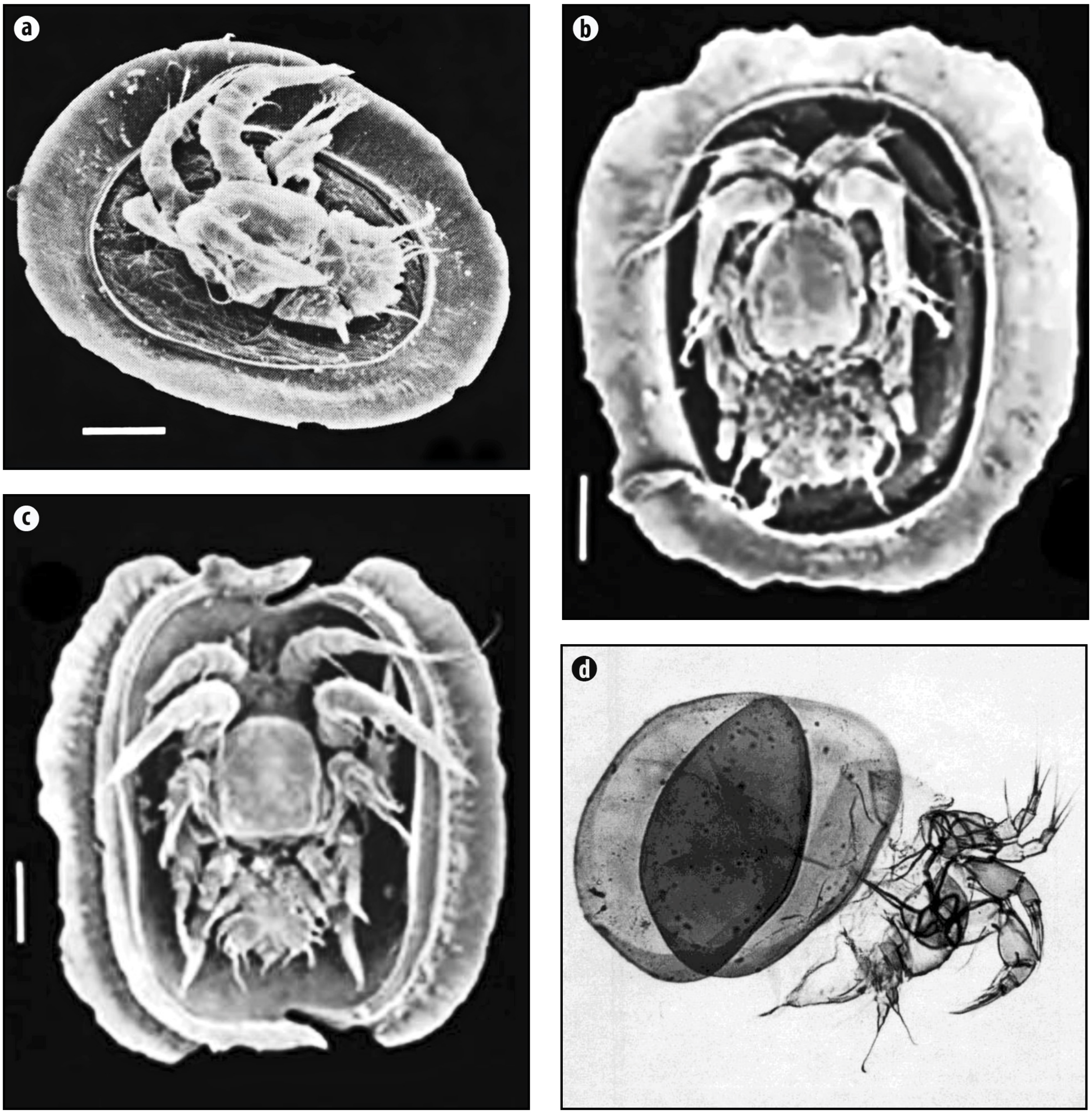


Figure 5. Postembryonal developmental stages of the ostracod carapace: **a-c** – *Manawa staceyi*, metanauplidus stages M1 – M3, l-side; **a** – M1; **b** – M2; **c** – M3; **d** – *Herpetocypris reptans,* cast skin of the A-8 instar (a-c, from Swanson, 1989b, D, from Harding, 1964).

the brush like organ (see Fig. 8c for morphological detail of same as exhibited by *Pussella botosaneanui* Danielopol, a podocopan bairdiod) is the homologue trait of the 8th ostracod limb. Hartmann (1966, p. 214) noted that brush like organs of cytherids (positioned between the 5th and the 6th limbs) are connected to a nervous ganglion placed near the hemipenis and which apparently acts also on the reduced 8th limb of the platycopid *C. sordida*.

We conclude that the similarity between the brush like organs of the podocopids and those of the puncioid *M. staceyi* is realised through parallel evolution due to deep homology structures. Therefore in all probability, this limb is not a uropod but a reduced thoracic limb.

3.3. Modular traits of the major Podocopa groups – Comparative analysis

Within the Subclass Podocopa Martin and Davis (2001) recognised two orders with living ostracods, the Platycopida and Podocopida, to this we propose to add a third Order Punciocopida, represented solely by living punciids. A comparative morphological analysis based on modular complexes is developed below.

Table 3. Characteristics of the body plans of the Subclasses Myodocopa and Podocopa.

Morphological & Functional Properties	Body plan 1	Body plan 2
Taxa	**Myodocopa**	**Podocopa**
Morphologic profile	Frontal polarity	Ventral polarity
Valves: Ventral margin	Most convex ventral margin	Straight or slightly concave
Valves asymmetry and overlap	Minimal	Commonly present
Ambulatory Limbs	Frontal positon for swimming	Ventral position for crawling
Antenna: Basipodite	Large musculous structure	Medium-long structure
Antenna: Endopodite	Reduced (gen. 2 articles)	Developed (gen. 4 articles)
Antenna: Exopodite	Well developed (7-9 articles)	Reduced (gen. 1-2 articles)
Male clasping organs	Endopodite of the A2	Endopodite of thoracic limbs
Maxillula: respiratory plate	Absent	Present
Thoracic limbs: L5 & & L6	Phylopodial epipodite	Stenopodial endopodite
Frontal (Belonci) organ	Present	Absent
Ocular structures (E)	Lateral E & Naupliar E	Only Naupliar E
Antennae aesthetascs	On the A1	On A1 and on endopodite A2
Position of furca	Posterior to anus	Anterior to anus
Circulatory organs	Part. Present	Absent
Developmental pattern	Fusion of 2 embryo buds	Splitting one embryo bud

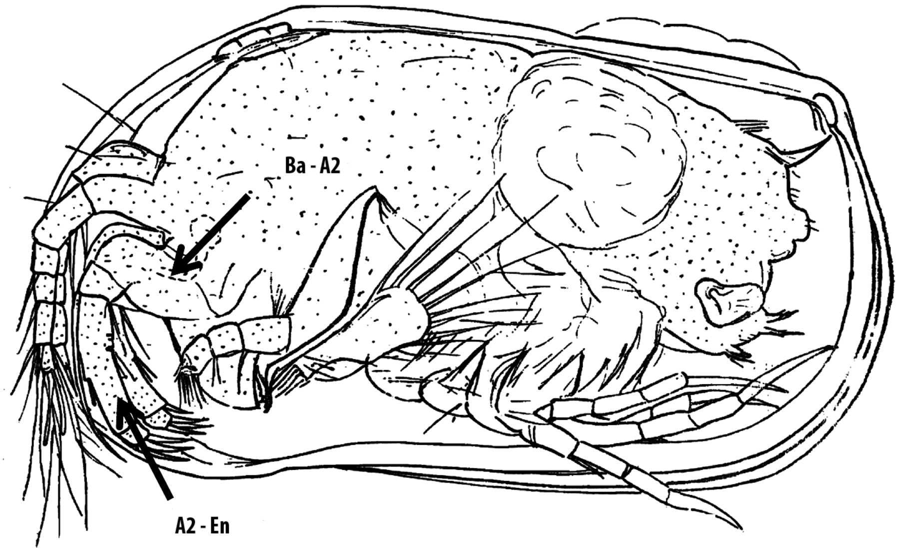


Figure 6. *Kovalevskiella phreaticola* Danielopol, general view, adult f.; Ba-A2 – Basipodite of the 2nd antenna; A2-En – Endopodite of the A2 (from Danielopol, 1970a).

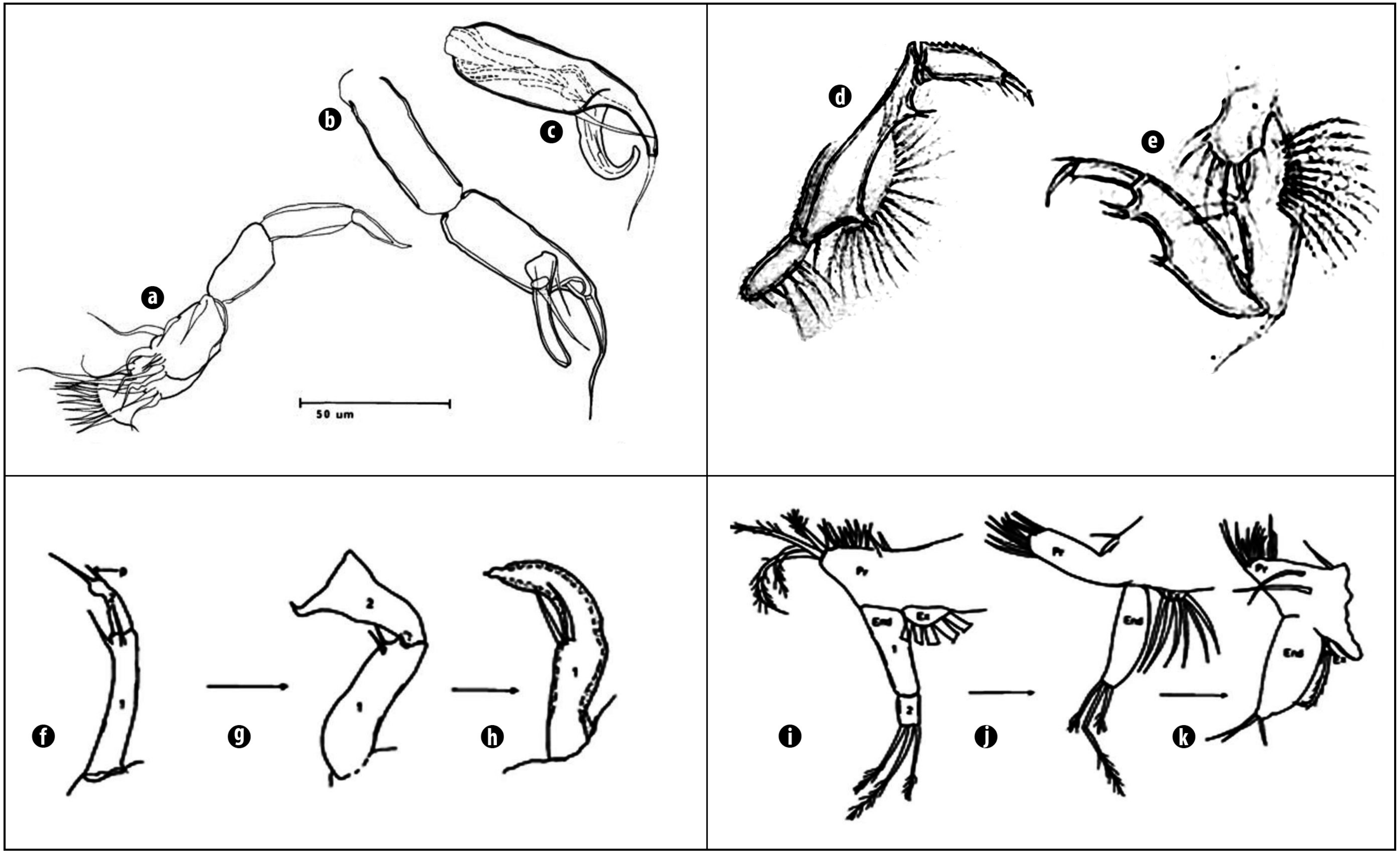


Figure 7. Endopodites of thoracic limbs: **a-c** – *Manawa staceyi*; **a** – f, pediform shape; **b**, **c** – m, left and right clasping organs; **d-e** – *Cytherella sordida*, m, L5 and L6 clasping organs; **f-h** – m, Podocopida clasping organs, various types; **f** – Ilyocyprididae; **g** – Cyprididae; **h** – Candonidae; **i-k** – f, pediform type; **i** – Ilyocyprididae; **j** – Cyprididae; **k** – Candonidae (a-c, from Swanson, 1989b; d-e, from Sars, 1923; f-k, from Danielopol, 1978).

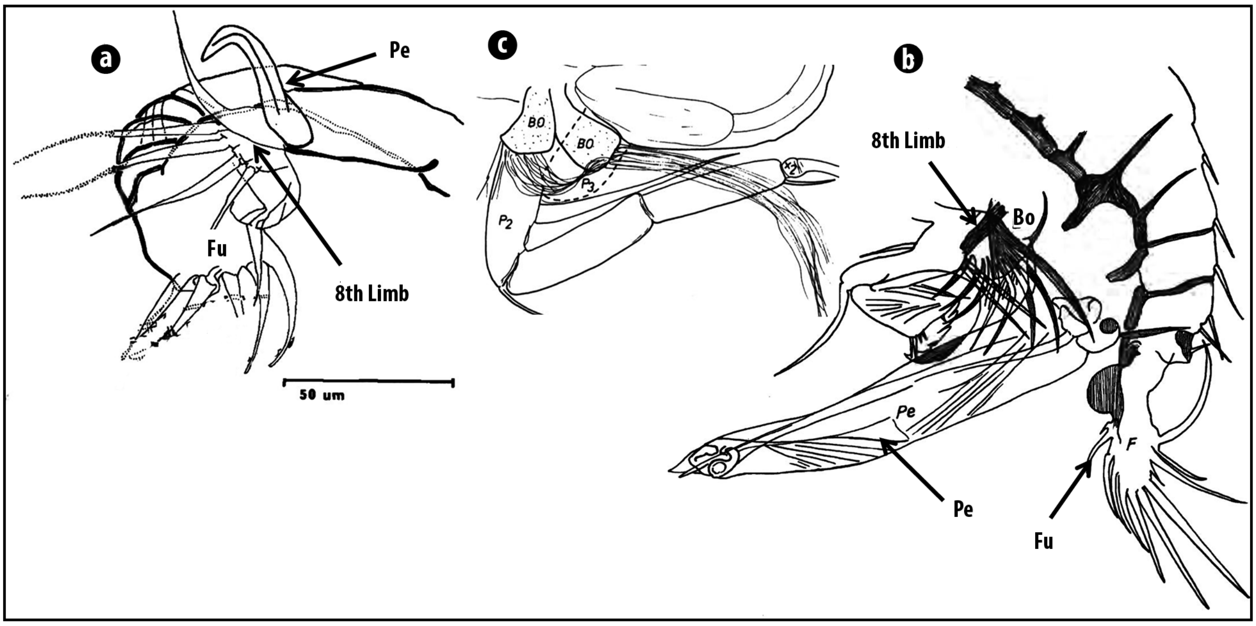


Figure 8. Brush-like organs limbs and copulatory organs, m: **a, b** – posterior of the body; **a** – *Manawa staceyi*; **b** – *Cytherella sordida*; **c** – *Pussella botosaneanui* (a, from Swanson, 1989b; b, from G.W. Müller, 1894; c, from Danielopol, 1976, symbols added).

3.3.1. The Carapace Module

The ostracod carapace represents a structural module which fully encapsulates that crustacean's soft body in order to protect it. As a general approach we will first discuss the properties of the carapace in which the structures of opposing valves display symmetry and/or close connections. The shape of the valves is an aspect of the similarity problem while the hinge structure offers an insight on the interconnection between the two valves.

The adults of the superfamily Puncioidea carry a lightly calcified carapace, which is slightly 'ornate' on the outer lamella. Nohara and Nakasone (1982) indicated that adult carapaces of *Promanawa konishii* Nohara display a slight sexual dimorphism. The female carapace is more inflated posteriorly than that of the male.

The two valves display minimal asymmetry in their general shape and slight differences in the structural morphology of the dorsal cardinal corners exist between the right and the left valve, namely the former one has two small plates named by Swanson (1989a) stragular processes (which do not occur on the left valve). This is well illustrated for *Manawa staceyi* (Figs. 2a,b, 9).

In general valves shape of the Puncioidea display ventrally a strongly arched outer margin that extends from the antero-dorsal corner to the posterior equivalent. The dorsal margin is straight-lined between the two dorsal cardinal corners (Fig. 1a-e, 10a).

During ambulatory excursions, the valves fully opened, leaving a ventral gape of about 180° (Fig. 2a). The ostracod now protrudes beyond the carapace with the ambulatory limbs assuming a lateral position (see details next section). A cluster of adductor muscles is placed on the upper half of the valves (Figs. 1a, b). Due to this position the valves can be fully extended as mentioned above. Swanson (1989a) showed that the stragular process, placed on the right valve of *Manawa staceyi* (Figs. 2b, 5c, 9) has an adaptive function, in that it helps prevent an over extension of the valves. It should also be noted that the straight dorsal margin of the valves was considered by Swanson (1989a) an adaptive trait enabling the transversal opening of the valves to a gape of about 180°.

The carapace of *Manawa staceyi* displays on its ventral side a peculiar structure of the marginal infold (*sensu* Yamada, 2007a). Extending inwards from the outer margin (Fig. 9) there is a smooth area on which a few normal pores emerge. It is assumed that this part of the marginal infold corresponds to the fused zone of the podocopids and the few normal pores and associated long setae are equivalent to the marginal pores and setae, as illustrated in Horne *et al.* (2002). Next, inside that smooth zone is a parallel area covered by numerous normal pores most of which are devoid of a seta. The boundary between these two areas could represent the so-called line of concrescence commonly present at the podocopids, bearing a free calcified inner lamella below which the vestibule occurs as in the of *Promanawa konishii* (Fig. 19e). A few, long sensorial setae however occur dispersed on the marginal infold (Fig. 19b) and it is assumed that these function during excursions over solid surfaces or during the mating when venter to venter copulatory position of the two sexes is adopted (Swanson, 1991, 1996).

A lamellar selvage runs inward, parallel to the outer margin, starting from the anterior dorso-ventral corner to the posterior one (Fig. 9; 10b). Inward a contact groove is visible, this delineated outside by the selvage, and on inner side by a ridge (similar to an inner list) which is located on the so-called inner margin (Yamada, 2007a). The soft inner lamella begins from the base of this peculiar inner margin (Fig.10b). The aspect of the so-called contact groove with the ridges of the selvage and the inner margin are similar on both valves (Fig. 9).

The carapace has an adont hinge. Hanai and Tabuki (1995) described the hinge of *Promanawa konishii* in which a thin elastic ligament is located between the antero- and postero-dorsal angles, and unites the two valves (Fig. 10b). The left valve at the anterior and posterior sides presents minute knobs dorso-ventrally, which corresponds to small pits found on the opposite valve. The hinge has no accommodation groove as in the case of podocopid ostracods.

The carapace of *Manawa staceyi* when valves are fully extended laterally resembles to geodesic dome, a solution used by the French architect Paul Andreu for his National-Grand-Theatre (opera house) opened 2007 in Beijing (Wikipedia: National Centre for the Performing Arts, China). As with the Andreu's construct, the carapace of *Manawa staceyi* exhibits structural stability (*sensu* Benson, 1965) when the animal assumes a transversal position despite the thin and spongious outer lamella, as well the occurrence of numerous normal pores that penetrate the wall of the outer lamella. The latter carrying one or two thin, non-perforated lamellae inside their channels (Fig. 12a-c). Hanai and Tabuchi (1985) made similar observations on the valves of *Promanawa konishii*, namely their fragility and the light in weight consistency of the outer lamella.

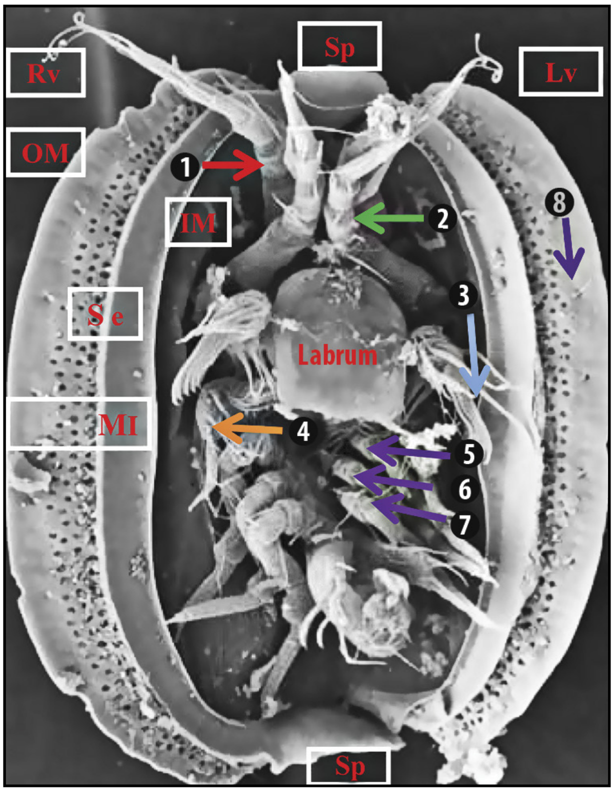


Figure 9. *Manawa staceyi,* carapace and body limbs, I f; OM-outer margin; Sp-Stragular process; Mi-marginal infold; Se-selvage; IM-inner Margin; 1-A1; 2-A2; 3-Md; 4-Mxl; 5-7 – L5-L7 thoracic limbs; 8- ventral marginal pore and seta (from Swanson, 1989b, symbols added).

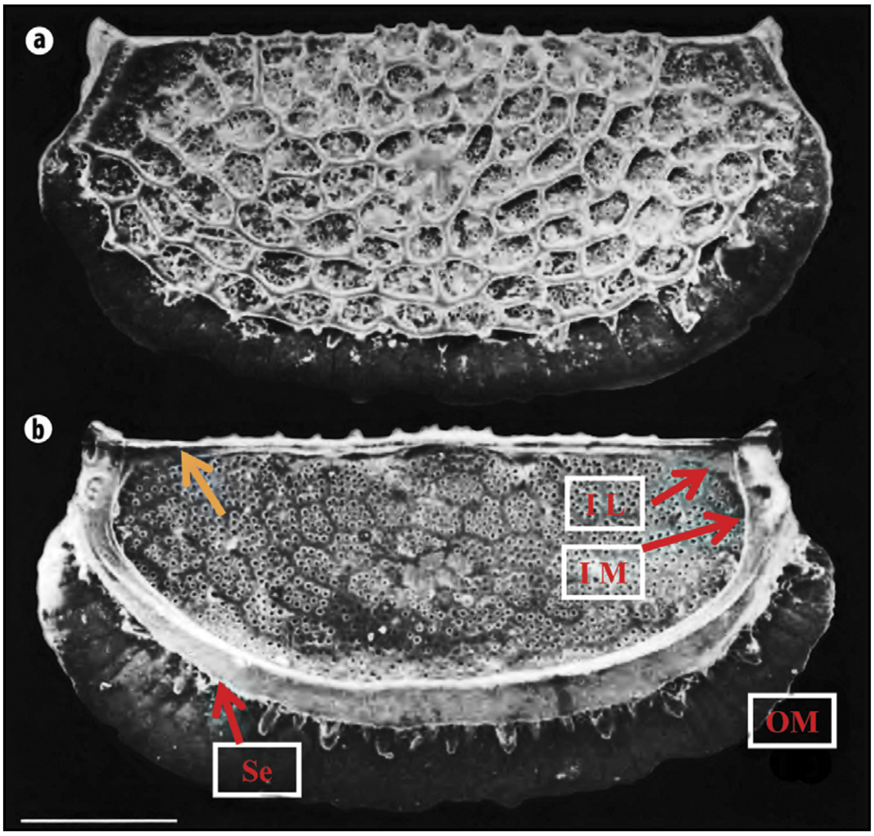


Figure 10. *Promanawa konishii***,** m, RV: **a** – E side; **b** – I side; OM-outer margin; MI-marginal infold; Se-selvage; IM-inner margin; IL-soft inner lamella; orange arrow point to the dorsal margin (from Hanai and Tabuki, 1995, symbols added).

The first stage of the post-embryonal development of the bivalve carapace is iniated with a single dorsal shield which encloses the entire soft anatomy (Fig. 5a, b). The two separate, articulated valves appearing after the third moulting at the metanauplius M3 (Fig. 5c).

The carapace of species of Platycopida are generally, strongly calcified and with a slight asymmetry. The carapace exhibits an obvious sexual dimorphism; the posterior third of the female's carapace being more inflated than that of the male. The ventral outer margin of the carapace is flat, a feature commonly found in those benthic crawling podocopes that penetrate inter-granular spaces of fine sediment. The valves during the ambulatory activity of the platycopids have a sagittal position. The intervalvar ligament lays on the dorsal and dorso-ventral margins. This special position determines that the valves have a narrow gape (of about 5-6°), with a more pronounced opening of the anterior portion of the carapace (Jaanusson, 1985). The adductor muscle scars lie in the central area of the valves, close to the median axis.

The carapace displays an adont hinge, the right valve presenting a peripheral furrow which also involves the section occupied by the intervalvar ligament. The outer ridge of the furrow is the valve's selvage, while the inner ridge is the inner margin. There is no development of hingement structures (*sensu* Yamada, 2007b). The posterior section of the selvage and of the inner margin are both ridge-shaped, thus forming an accommodation furrow which continues along the dorsal margin.

The contact furrow is more attenuated on the antero-ventral section of the valve, as the ridge of the inner margin diminishes. The left valve has a well-developed selvage while the inner margin displays a visible ridge only on the postero-dorsal section of the marginal infold. This inner margin ridge is the equivalent positive structure which is inserted in the contact groove of the right valve. An excellent visualisation of the relationship between the selvage and the inner margin for the right and left valves of a platycopid was presented by Tsukagoshi *et al.* (2006, Fig. 6).

No vestibulae exist and the normal pores of platycopids do not include sieve-type pore canals. Okada *et al.* (2008) showed that in the first post-embryonal stage of the platycopid *Keijcyoidea infralitoralis* Tsukagoshi, Okada and Horne two separate valves have already developed.

Podocopidid ostracods exhibit a wide range of carapace forms, these often with asymmetrical valves. The ventral area of the carapace is in many cases flat. A bow-shape process exists on both valves in the central part of the ventral margin (Fig. 11a, b). The selvage is generally well developed and the inner margin has no ridge. Instead, some podocopid ostracod groups have valves with an inner list positioned on the marginal infold between the selvage and the inner margin. The inner, soft lamella articulates directly on the flat inner margin. The hinge is well delineated on the dorsal side of the valves, occurs in a wide diversity of morphologies (which are often of taxonomic significance) (*sensu* Yamada, 2007b). For instance in some taxa, on the dorsal anterior and posterior sides one finds teeth that are accomdated by sockets in the opposite valve. Between the cardinal corners of the dorsal margin one finds a smooth or denticulate, intercardinal bar, which fits the intercardinal groove formed by ridges in the opposite valve. The upper ridge is a continuation of the selvage, while the lower equivalent (a strong ridge) is the continuation of the inner margin of the marginal infold. In this way the podocopid hinge differs markedly from those of the punciids and the platycopids. Danielopol, Piller and Gross (MS in preparation) illustrate the details of the podocopid hinge-type using *Cytheridella ilosvayi* Daday (*sensu lato*) as the exemplar.

The adductor muscle scars lie in the central area of the two valves and these open ventrally to a maximum gape of about 30° (Figs. 11a, b). During ambulatory activity, podocopids maintain the carapace in a vertical (or sagittal) position, as in the case for platycopids.

The outer lamella on both valves has normal pores with sensorial setae. In the case of Cythericopina one finds the so-called sieve-type pore canals, (Danielopol *et al.*, 2018; Lord *et al.*, in press). These StPC present a perforated calcified lamella which are extremely diverse with respect to both shape and the number of the minute tubules displayed.

Significantly, the timing of the separation of the two valves during the post-embryonal development varies between taxa. Horne *et al.* (2004) discovered that for *Terrestricythere elisabethae* Horne, Smith, Whittaker and Murray the bivalve carapace has already formed in the first instar stage. That situation is repeated in *Uncynocythere occidentalis* Kozloff and Whitmann as described by Smith and Kamiya (2005). In the case of *Darwinula stevensoni* Brady and Robertson, it was shown by Smith and Kamiya (2008) that the two calcified valves are formed only in the second instar stage. The same is apparently the case of *Herpetocypris reptans* (Baird) (Fig. 5d) studied by Harding (1964).

3.3.2. The Ambulatory Module, combined with the Feeding Module

Manawa staceyi undertakes ambulatory excursions both on and within benthic substrates, mainly using the antenna and the 5th to 7th trunk limbs to achieve same (Swanson, 1989a). The role of the antennule with its few distal setae (Fig. 16a) and of the furca (Fig. 8) seems to be a supplementary one. The endopodites of the A2 and the L5 – L7 display a short claw-like dactylus (Fig. 13b-d). Characteristic for the antenna is an elongated carpus (the 3rd podomere) (Fig. 16b), pectinated on the inner side (see arrow), this, an apparent adaptation for gathering minute food particles and directing them to the mouth. The merus (the 2nd podomere) carry short, undifferentiated distal setae which are homologues to the swimming setae of cypridoid Podocopida. The endopodites

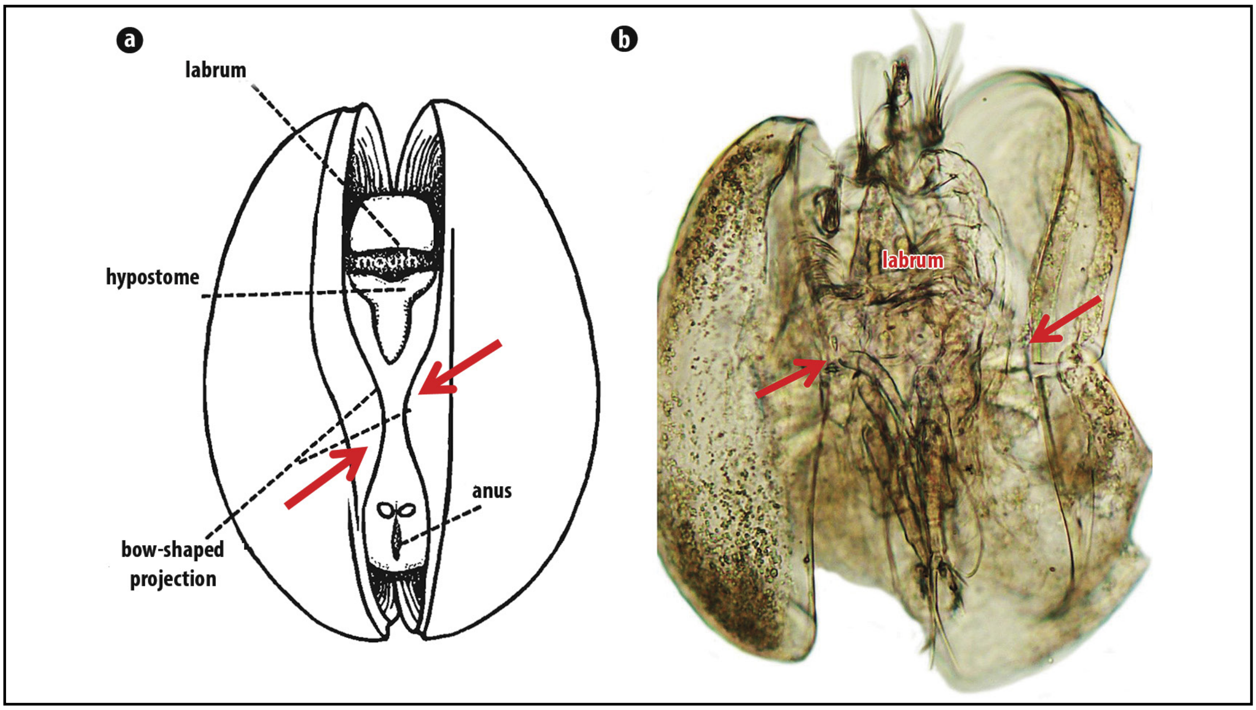


Figure 11. Podocopid ostracods, ventral view, showing typical carapace gapes: **a** – *Cypridopsis vidua*, f; **b** – *Saipanetta* sp., j (a, from Cannon, 1926, redrawn by Adamczak, 1969; b, unpublished photo, courtesy of Rosalie Maddocks, arrows added).

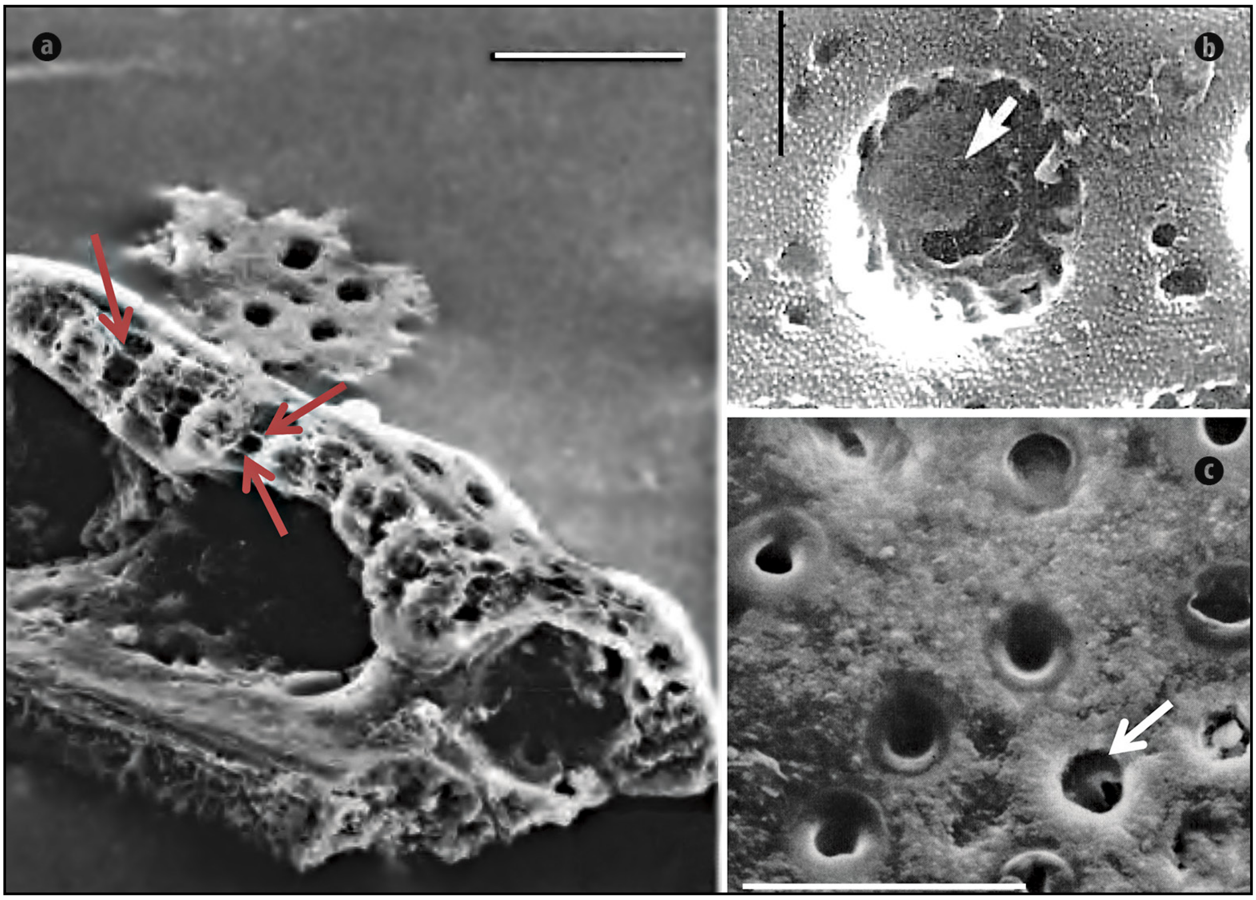


Figure 12. *Manawa staceyi* (**a, b**) and *Promanawa konishii* (**c**), morphology of the valve: **a** – section through the calcified outer lamella and normal pores (arrows point to transversal lamellae); **b** – aperture of normal pores on the outer side of the valve (arrow points to a broken transversal lamella); **c** – aperture of normal pores on the inner side of the valve (arrow points to a transversal lamella inside the pore); scale bars: A-0.025mm, B-0.004, C-0.01mm (a-b, from Swanson, 1989a, c, from Hanai and Tabuki, 1995, arrows added).

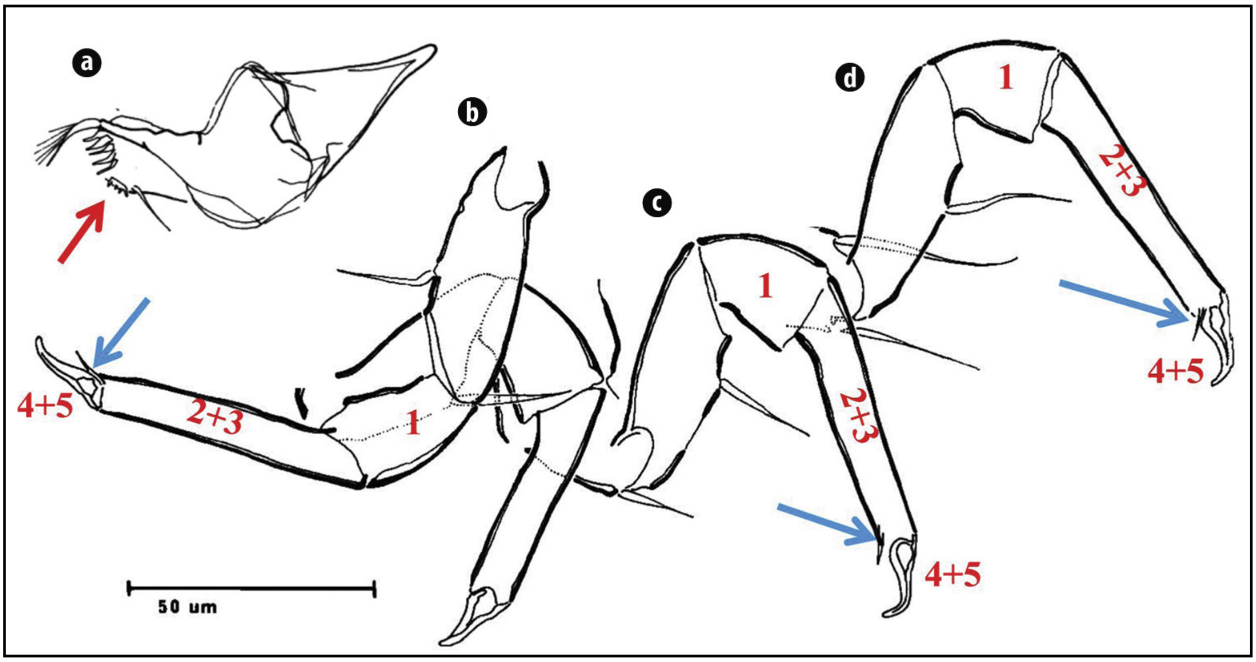


Figure 13. *Manawa staceyi*: mandible (**a**) and thoracic limbs L5 to L7 (**b-d**); **a** – mandible with details of the gnathobasis (arrow points to the inner "grinding" segment); **b-d –** details of the endopodites (arrows point to the minute seta which is a reference point for the delineation of the 3rd and the 4th endopodial podomeres) (from Swanson, 1989b, arrows added).

of the L5 to L7 display the 2nd with the 3rd podomere fused and forming an elongated endopodial segment which distally bears a short seta (Fig. 13b-d). The latter being a characteristic of podocopid ostracods as a reference for the limit between the 3rd (carpus) and the 4th (propodus) podomeres. The latter in *Manawa* is further fused to the dactylus. When the valves are extended to an approximately 180°gape, the second antenna and the thoracic limbs are then extended laterally. The body remaining very close to the substrate and the movement of the animal is slow, "armadillo like" with side-to-side rocking motion (Swanson, 1989a).

One has to mention the rectangular, flat labrum (Fig. 9, 16g), appropriate with respect to the position the animal assumes when stationary on a solid substrate. Also of interest, is the structure of the mandibular gnathobasis with its distal side displaying an outer, cutting area with strong denticles and a short spiniform, plate-like device on the inner side (Fig. 13a). This special morphological structure suggests that the food gathered by *Manawa staceyi* is a mixture of solid organic particles of varying size. Swanson (1989a; 1989b) illustrated sediment accumulation in front of the mouth opening and the labrum. The food particles are brought to the mouth by the long pectinate antennae and the mandibular endopodite with long distal setae (Figs 9, 16b, f). Therefore, *Manawa staceyi* is a deposit feeding ostracod (*sensu* Cannon, 1926).

The platycopid ostracods, such as *Cytherella abyssorum* Sars (Fig. 15a), for walking use mainly the antennae (A1 and A2) and the furca (Sars, 1923; Tsukagoshi *et al.* 2006). The antennule and the exopodite of the antenna especially, are very strong being used for digging into the substrate. The movement of platycopids is slow and Jaanusson (1985) pointed out, that a lower number of muscles acting on limbs are used than is the case for podocopid ostracods. One should note here that the gathered food particles are chewed with a distal gnathal process which has only one row of spinules (Sars, 1923; Tsukagoshi *et al.*, 2006). The latter authors, showed that platycopids feed on solid organic microparticles deposited in front of the mouth.

The Podocopida carry ambulatory limbs, these represented by the antenna, with a strong pediform endopodite displaying diverse chaetotaxic patterns and thoracic limbs. The limbs L5 to L7, or at least one or two of same, are pediform and actively used for movement on/in benthic substrates (Figs. 15b,c). In general, podocopids display endopodites on which the first three podomeres are approximately equal in length and long dactyli (Figs. 14c, f-h). An exception to the long dactyli pattern as an adaptation for moving across fine sediment or solid substrates, occurs in those benthic ostracods which have adapted to a life in unstable benthic marine substrates exposed to strong currents, (e.g. *Xestoleberis exmouthensis* Hartmann (Hartmann, 1978) which displays short claws-like dactyli for gripping and anchoring to substrate particulates/surfaces. An analogous solution exists in phoretic ostracods such as Entocytheridae (Danielopol, 1971). For comparative purposes we illustrate here (Fig. 14) the adaptive solution for ambulatory activities on the deep-sea benthic substrates, as expressed by *Anchistrocheles angulata* (Brady), a bairdioid species living in a stable, fine-grained sedimentary environment. One should note the elongation of the distal dactyli located on the A2 and L5 – L7 endopodites.

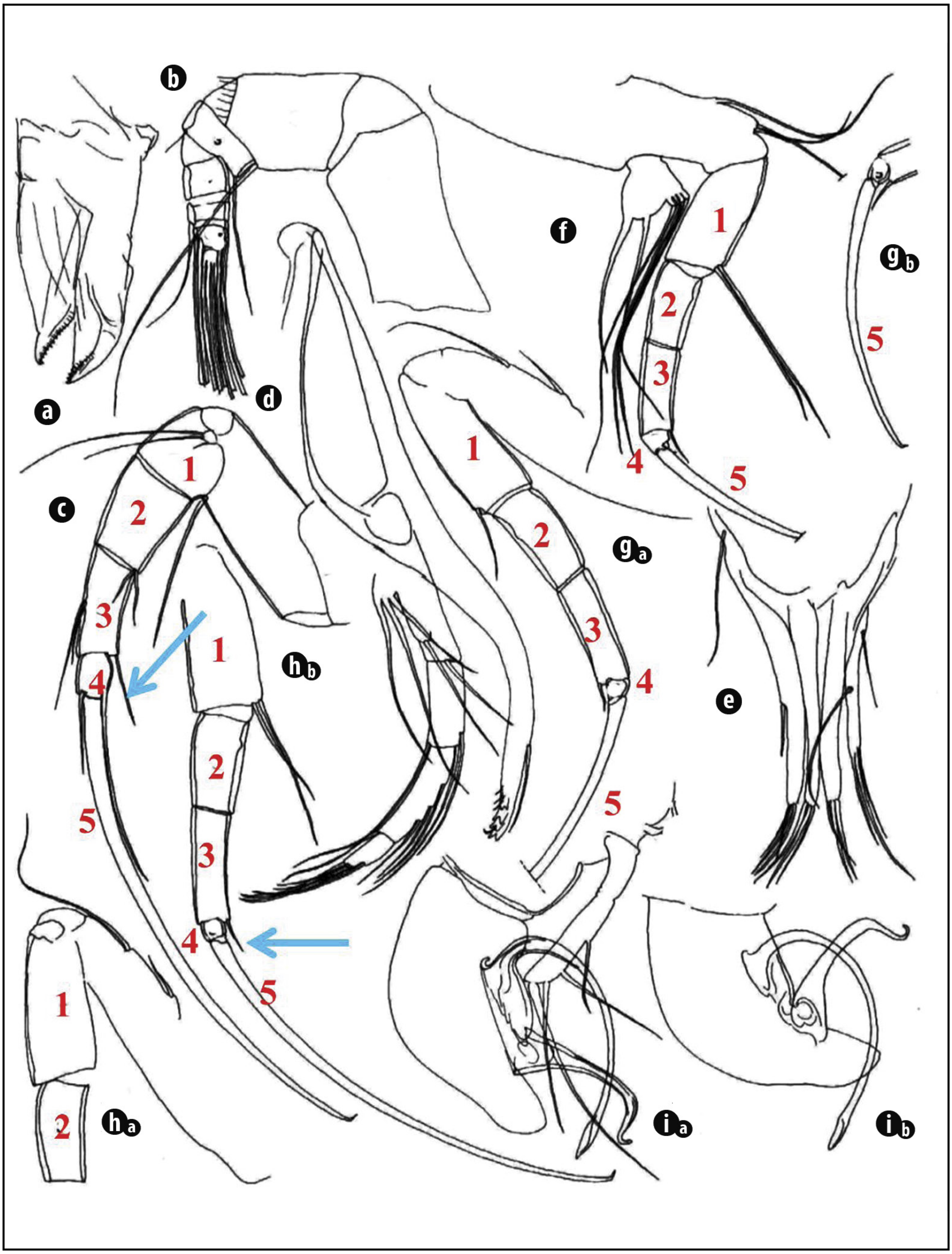


Figure 14. *Anchistrocheles angulata* (Brady), details of the limbs: **a** – upper and lower lips of the mouth; **b** – antennule; **c** – antenna; **d** – mandible; **e** – maxillule; **f** – L5; $\mathbf{g_a}$ & $\mathbf{g_b}$ – L6; $\mathbf{h_a}$ & $\mathbf{h_b}$ – L7 (blue arrow indication, as in figure 13); $\mathbf{i_a}$ & $\mathbf{i_b}$ –hemipenes (from Maddocks, 1976, arrows added).

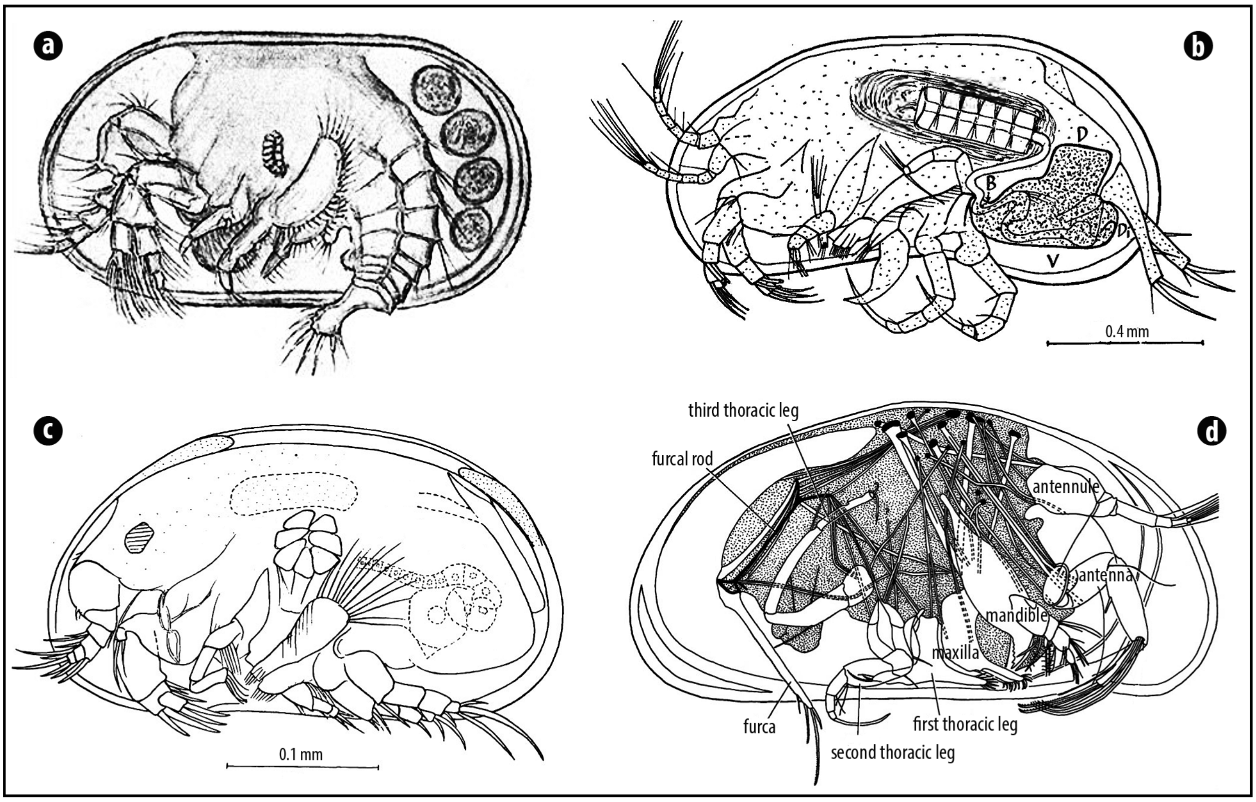


Figure 15. Platycopid (**a**) and podocopid (**b-d**) ostracods, comparative morphology of structures used for ambulatory activities: **a** – *Cytherella sordida,* f; **b** – *Candona neglecta*, m; **c** – *Microdarwinula zimmeri*, f; **d** – *Chlamydotheca arcuata*, f (a, from Sars, 1923, b, from Danielopol, 1969, c, from Danielopol, 1968, d, from Smith, 1965).

The mandibular gnathobasis of podocopids bears strong lamellar teeth on the external side of the gnathal process (Danielopol, 1970b), while the inner part of that process only sometimes carries spines (*cf.* for Macrocypridoidae, Maddocks, 1990). Smith (2000) showed that the podocopid labrum, in ventral view, appears slightly convex and is roughly triangular in shape. We illustrate herein the labrum of *Saipanetta* sp. (Fig. 11b) and of *Anchistrocheles angulata* (Fig. 14a). The musculature of the podocopids acting on the limbs engaged in walking or swimming movements (Fig. 15d) are more highly developed (Smith, 1965) than those mentioned above for platycopids.

3.3.3. The Mating Module

Swanson (1989b) showed that *Manawa staceyi*, displays a very simple elongate copulatory process activated by strong muscles attached to the basis (Fig. 19c). Interestingly, this organ (generally represented by symmetric hemipenes) in the case of the punciids occurs only on the right side (Fig. 8a). It is located in front of the 8th limb (Swanson 1989b) suggesting a thoracic origin. It is also important to acknowledge the mating position of *Manawa staceyi* in which the copula is represented by venter to venter contact with valves of both sexes fully gaping to 180° (Swanson, 1996).

Ostracods of the Order Podocopida display penes with a wide range of morphologic traits which are involved in processes associated with both female recognition and mating (*cf. inter alia* Danielopol, 1969; Martens, 1990; Horne *et al.*, 1998 and herein, the hemipenes of the bairdioid *Anchistrocheles angulata,* Figs. 14i_a, i_b). Horne *et al.* (1998) showed that in the case of cypridoids the male copulates by keeping the female in a ventro-posterior position with carapaces having only a narrow gape. A ventro-to-ventral position where the carapaces display a narrow gape was also observed, as in the case of Cypridoidea Candonidae (Danielopol, 1980). Herein we illustrate the case of the bairdioid *Pussella botosaneanui* (Fig. 19d).

Males of the various species of the Order Platycopida display also elongated and muscular hemipenes, located symmetrically on the sides of the body. The distal part of the hemipenis (Fig. 8b) bears morphologic structures that play a role in species recognition (Swanson, 1993; Swanson *et al.*, 2005). The latter author also noted that the male copulatory organ of cytherellids has to be viewed as the protopodite of a thoracic limb. A similar case exists in the case of the crustaceans belonging to the Malacostaca Podophalocarida (Serban, 1972).

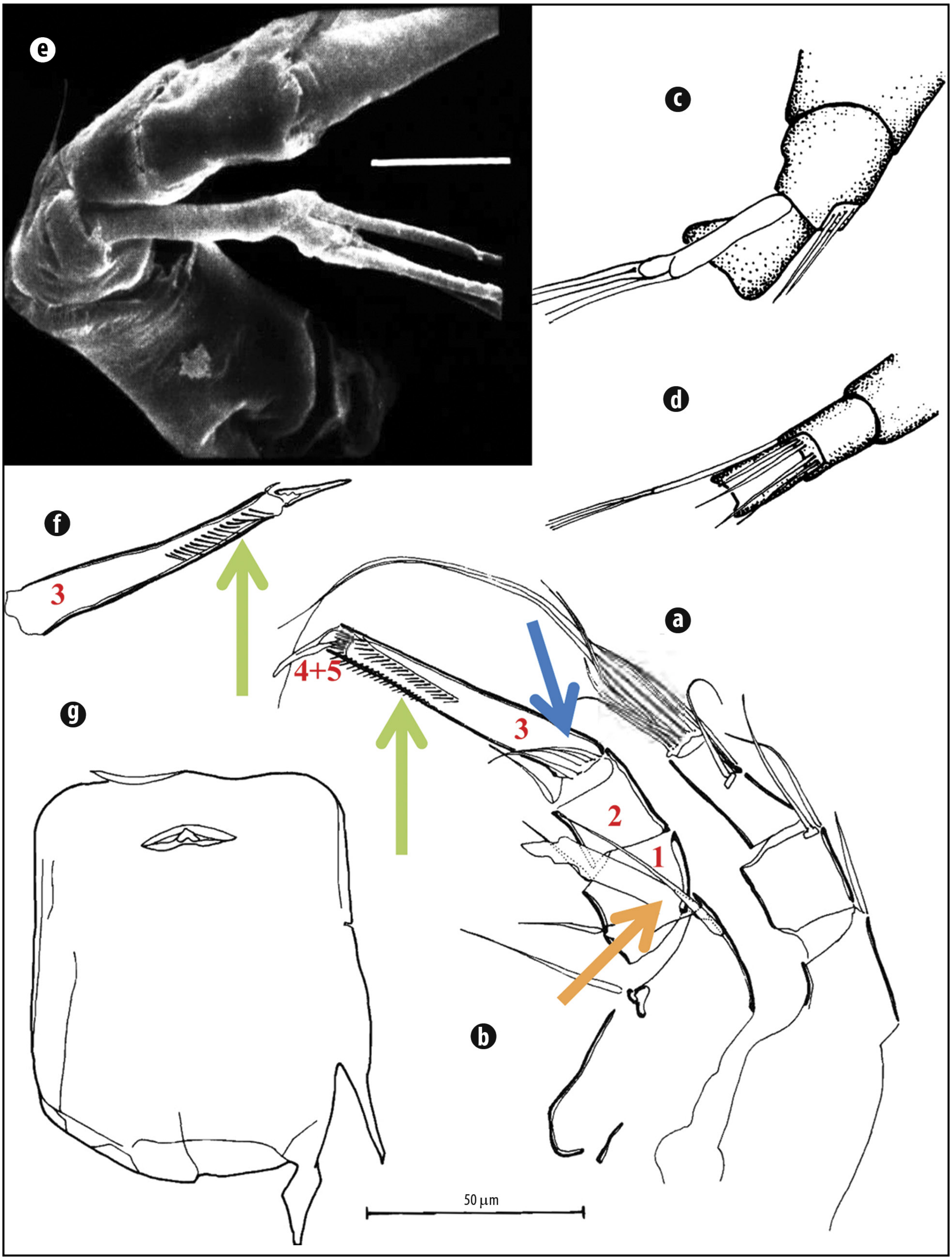


Figure 16. *Manawa staceyi*, morphology of the antennae and labrum: **a** – antennule; **b-f** – details of the antenna; **g** – labrum; **b** – A2, general aspect; **c,e** – exopodite; **d,f** – podomeres of the endopodite (orange and green arrows point to the exopodite, respectively to the pectinate endopodite; blue arrow points to homologue t setae as in Fig. 17) (from Swanson, 1989b, arrows added).

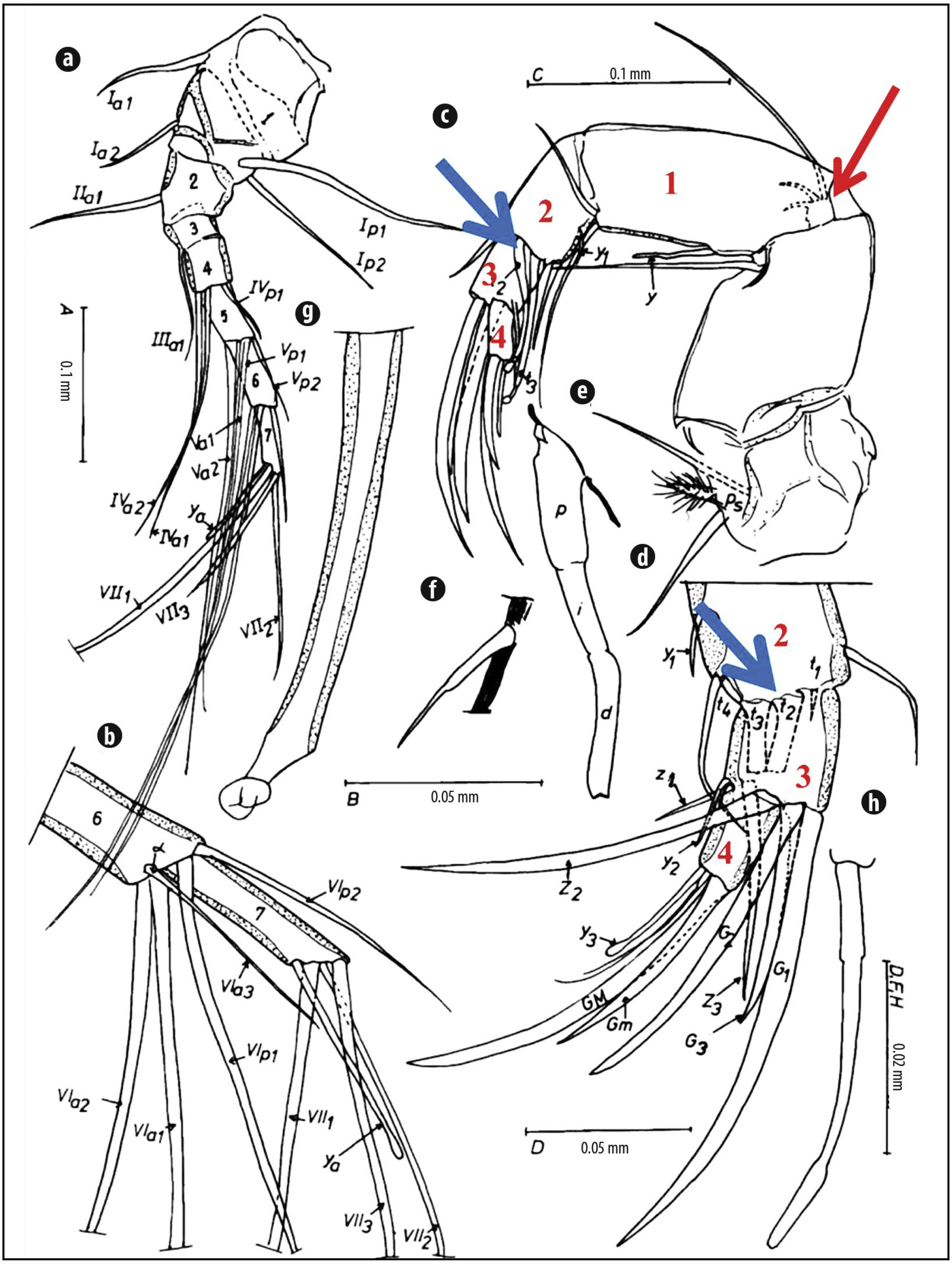


Figure 17. *Candona sanociensis*, m, morphology of the antennae: **a,b** – antennule; **a** – general aspect; **b** – detail of the distal podomeres with the aesthetasc "ya"; **c-h** – antenna; **c** – general aspect; **d** – detail of the endopodite; **e** – aesthetasc "Y"; **f** – aesthetasc "y1"; **g** – detail of the "t2" seta; **h** – aesthetasc "y3" (from Danielopol, 1978, arrow added: the blue one points to the t setae, the red one, to the antennal exopodite with its typical setae).

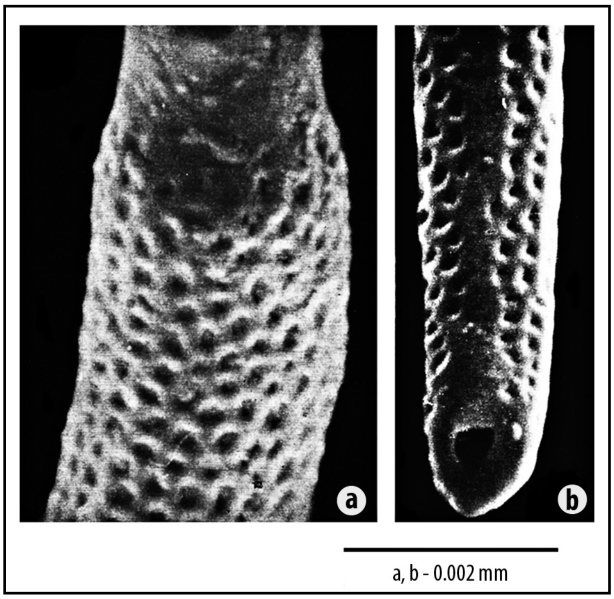


Figure 18. *Candona sanociensis*, m, details of the chemosensorial section of the aesthaetasc "Y": (**a**) and "y3" (**b**) (from Danielopol, 1973).

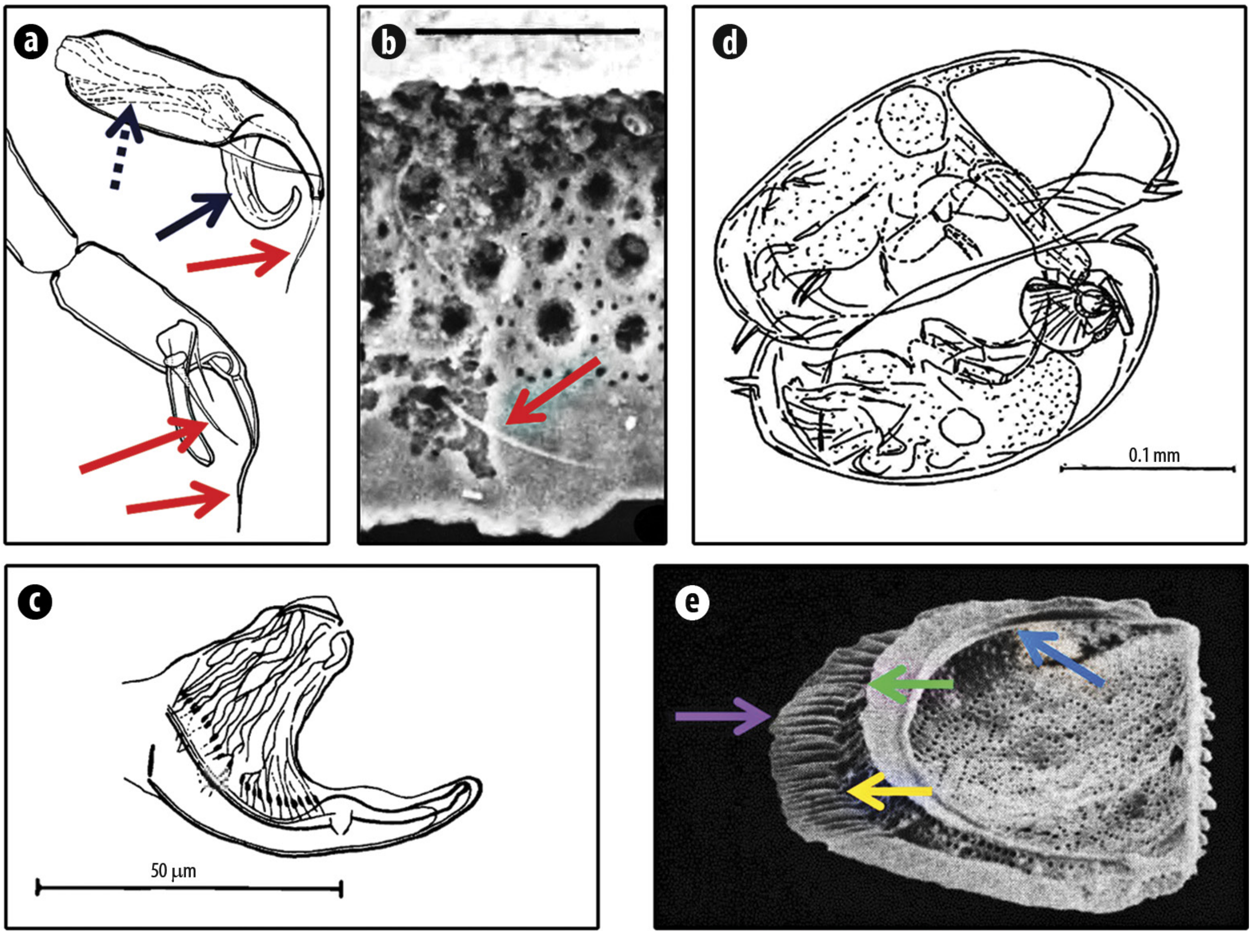


Figure 19. Morphologic aspects of *Manawa staceyi*, m (**a-c**), *Pussella botosaneanui* (**d**) and *Promanawa konishii* (**e**): **a** – maxillular clasping organs (blue arrow indicates the movable distal finger, dashed arrow points to the muscles acting on the movable finger, red arrows indicate the sensorial setae); **b** – ventral seta on the marginal infold (see red arrow) possibly used during the act of matting; **c** – right hemipenis with muscles; **d** – ostracods f &m fixed in copula ventral to ventral position; **e** – anterior part I, RV (arrows: violet point to the outer margin, yellow indicates the line of fusion, green, the selvage, blue the inner margin). (a-c,from Swanson1989b; d, from Danielopol, 1976; e, form Hanai and Tabuki, 1995, arrows added).

The sensorial system found in male ostracods is represented by morphological structures of the penes and by those occurring on transformed endopodites of the thoracic limbs. In the case *Manawa staceyi* we highlight the presence a clasping organ with a movable claw and long setae on the maxillula (Fig. 19a). A similar articulated claw is known to occur on the 5th limb of the males of the podocopid Macrocypridoidea (Maddocks, 1990). The distal seta of the clasping organ of *Manawa staceyi* (Fig. 19a), probably plays a sensorial role by touching the female during the mate process. A similar seta occurs on the 5th limb of the clasping organ of the Cypridoidea Ilyocyprididae (Fig. 7f).

Manawa staceyi displays on the marginal infold (Figs. 9, 19b) long setae which following Swanson (1989a) also play a sensorial role during the mating process.

Platycopids have two pairs of clasping organs on the 5th and 6th limbs on which short setae exist for tactile engagements with the female (Fig. 7d). In the case of the Podocopida, the 5th limb of the Cypridoidea and the Macrocypridoidea also carry clasping organs with short sensorial setae and/or a distal touching peg (Figs. 7f-h). Their role is to 'stimulate' the female during the mating process. Similar touching behaviour of the male using the 5th limb is described by Abe and Vannier (1993) for two podocopid cytheroids; and this was interpreted as a type of courtship behaviour.

The males of Cypridoidea Candonidae and of Macrocypridoidea display two strong setae (the t-2 and t-3) on the 2nd endopodial podomere of the antenna. These setae have on their apical side round papillae (Fig. 17c, g). Their role is also to touch the female during the mating process.

3.4. The rarity of Puncioidea taxa as compared to non-marine Cypridoidea

The superfamily Puncioidea is represented by few taxa, namely two families, the Punciidae Hornibrook, 1949 and Triassopunciidae Kozur, 1998, six genera and 16 species of which ten are known only as fossil. There is only one species for which we know the morphology for both valves and limbs, namely *Manawa staceyi*, Swanson. Tables 2 and 5 which as a result, offers a general view of this group. It is important to mention that the superfamily Puncioidea displays a both a wide geographic distribution and a very long history with respect to the geologic record (Table 2). Recent and Neogene punciids have been recorded along the coasts of Australia, New Zealand and Japan. Triassic and Cretaceous taxa have been recovered in Central and Northern Europe (Table 2).

The low taxonomic diversity of the Puncioidea (16 species) becomes obvious when one compares it with the species richness of the podocopid Cypridoidea (Table 5). The latter group being represented by about 1750 species belonging to four families. The species richness of the families Cyprididae and Candonidae represents 95.5% of the total number of cypridoid species listed by Meisch *et al.* (2019).

An explanation for the conspicuous difference between the superfamilies Puncioidea and Cypridoidea will be presented in the next part of this contribution.

4. DISCUSSION

4.1. The morphological profile of *Manawa Staceyi* – a reappraisal

The general morphology of *Manawa staceyi* was used within this project as reference for the entire superfamily Puncioidea and by extension, to the Order Puncioсopida Schallreuter, 1968, which is taxonomically defined in the next section. Following the information presented by the disassembly of a general morphology into quasi-independent morphological modules, we will now proceed to a synthesis of the resultant data in order to get an image equivalent to a body plan. Table 4 lists the main information that will be further developed so that a comparison with the already presented body plans of the Myodocopa and Podocopa may be achieved.

In general from the modular analysis we conclude that *Manawa staceyi* is a reflection of that profile attributable to the body plan of Podocopa. It has a ventral polarity of the limbs, the antenna are elongated without musculous basipodite. The valves are light, in the sense of being moderately calcified and with numerous normal pores. A weak asymmetry of the dorsal cardinal area exists as a result of the so called stragular process found only on the right valve. Despite the fact that the ventral margin is convex displaying a velum with frills, this ostracod is a benthic crawler. But the fundamental difference between typical podocopes and *Manawa staceyi* is the horizontal position of the open valves achieved when they gape at approximately 180°. This opening is possible as a result of the positioning of the adductor muscles of the valves above the mid–height (dorsally).

Until now, the morphology of *Manawa staceyi* was considered, as compared to those of the highly morphological diverse Podocopida, as containing primitive ostracod character traits (discussion in Swanson, 1991, Becker and Swanson, 1992). The presence of an 8th limb considered as uropod, the posterior part of the body segmented, and the valves with a long transversal dorsal hinge being seen as evidence for same. Similarly, the separation of the two valves during the postembryonal development of the carapace (completed much later than in the case of most of the Podocopa) was also seen as compelling. As additional evidence, the valve morphology of the punciids was seen to most resemble Palaeozoic ostracods belonging to Palaeocopa ostracod groups, such as the kirkbyocopids and/or the beyrichiocopids. This observation drawing the attention of a number of ostracodologists, including; Hornibrook (1949), Schallreuter (1968), Swanson (1991), Becker (in Becker and Swanson, 1992). However, the exact

Table 4. Body plan of Punciocopida.

Morphological & Functional Properties	Body plan 2a
Taxon	Punciocopida
Profile	Ventro-Lateral polarity
Valves: Adductor muscle imprints	Above the middle height of the valve
Valves ventral margin	Convex margin
Normal pores on valves	Canals with 1-2 thin plates
L/R Valve-overlap	No valve overlap
Antenna (A2): Basipodite	Medium-long structure
Antenna (A2): Endopodite	Well developed (3rd article long and inner pectinated)
Antenna (A2): Exopodite	Elongated, 2 articles, 3 long setae
Male clasping organs-location	On Maxillular endopodite
Maxillule: respiratory plate	Absent
Endopodite of L5 & L7 limbs	Stenopodial type
Ocular structures	Not visible (probably reduced)
Position of furca	Anterior to anus
Orientation of ambulatory limbs	Ventro-lateral position under activity
Sensorial organs (aesthetascs)	Absent
Bi-valves & hinge completion	At Instar "4" (3rd metanauplius)

Table 5. Number of Puncioidea species versus living non-marine ostracod species belonging to superfamily Cypridoidea and its families. Data for Puncioidea from Table 2 and for Cypridoidea from Meisch *et al.* (2019).

Superfamily	N°. of species	Family	N°. of species
A – Puncioidea	16		
		Punciidae	12
		Triassopunciidae	4
B – Non-marine			
Cypridoidea	1760		
		Cyprididae	1006
		Candonidae	675
		Ilyocyprididae	41
		Notodromatidae	38

Note: For Cypridoidea only taxa with at least 35 species are recorded.

phylogenetic relationships between Puncioidea and the Palaeozoic ostracods remained elusive. Swanson (in Becker and Swanson, 1992) defended the idea that the profile of the punciids is plesiomorphic to those of other palaeocope kirkyocopids, while Becker in the same publication (op. cit.) argued the opposite, suggesting, the Palaeozoic kirkbyocopids display more plesiomorphic traits than the punciids and no direct phyletic relations between the two groups exists. The consideration of Puncioidea as a more primitive group compared to the kirkbyocopids (Swanson, op. cit.) had an intuitive appeal for the time when this hypothesis was advanced. During the early 1990's, bradoriids and phosphatocopids, with superficial morphological similarities to the carapace of punciids, were still considered to belong to the Class Ostracoda (Whatley *et al.*, 1993). However, that situation has changed dramatically, nowadays both Bradorida and Phosphatocopida, represent arthropod lineages, phyletically separated from the Ostracoda (Maas, 2003; Hou *et al.*, 2010; Betts *et al.*, 2015; Zhai *et al.*, 2019). The contention of Becker (in Becker and Swanson, 1992) gains again more plausibility, when one considers, as here argued, that Puncioidea is an ostracod group belonging to the Subclass Podocopa, and, that the Class Ostracoda is accepted as a monphyletic group. Within such a framework, because in both Subclasses Myodocopa and Podocopa, constituent species have generally adopted a sagittal (or vertical) carapace orientation and a narrow gape during the ambulatory excursions, one has to adopt Becker's hypothesis that kirkbyocopids display a more plesiomorphic state when compared to the puncioids.

The 8th limb considered a uropod *de facto,* is homologous with a regressed thoracic limb as occurs in the Orders Podocopida and Platycopida (Hartmann, 1966), while the segmented trunk of *Manawa staceyi* represents a homology of a similar structure that occurs in platycopids, and as visible remnants in some of podocopid groups (Tsukagoshi and Parker, 2000; Tsukagoshi at al., 2006).

The absence of the left hemipenis may be due to a structural reduction, reflecting the life of these ostracods occupying the intergranular spaces of marine sediments. A similar adaptive solution was documented by Hartmann (1973) in a mesopsammic cytheroid *Parvocythere dimorpha* Hartmann. An alternative explanation for the origin of the asymmetry of the hemipenis of *Manawa staceyi* may be that this is the result of a deep homology-related process that exists at a higher level in the phylogenetic hierarchy. A single hemipenis also occurs in Cladocopida (Myodocopa). Therefore, these traits cannot be considered as evidence for a primitive state of *Manawa* and by extension, the Puncioidea. Rather, they suggest that both kirkbyocopines and puncioids are two phylogenetic lineages with specialised morphologic traits, and these, most probably derived from a more primitive, yet undiscovered Palaeozoic group, as presumed by Swanson (in Becker and Swanson, 1992).

As a continuation of the discussion surrounding the comparative morphology of the main Podocopa groups, we will now draw attention to an interesting feature on the mandibular gnathobasis. This appears specialised for both cutting and grinding. When compared to the gnathobasis of platycopids (which have only one type of spinule), those of *Manawa staceyi* appear more similar to those found within ostracod taxa belonging to the Order Podocopida, specifically darwinulids and macrocypridids.

The morphological profile of *Manawa staceyi* briefly presented above suggests another view, namely that this ostracod species displays traits which represent adaptive solutions to the environment where it was discovered and sampled alive, namely a benthic marine habitat with coarse granular sediment, strong water currents, vis a very dynamic benthic habitat. The lack of a respiratory maxillular plate may be related to the niche of the animal, adapted to stay closer to the substrate, being in this way protected against the movable sandy grains. The body facies of *Manawa staceyi* is typical for psammobionts as characterised by Giere (1993).

Under laboratory conditions Swanson noticed (unpublished information) that *Manawa staceyi* when mechanically disturbed, reacts by closing partly the valves and then moving into the interstitial space of the granular substrate. This means that a punciid species is not only able to adopt the horizontal position with wide gape when moving on a substrate (typical for epipsammic animals), but can also assume the vertical orientation most commonly associated with podocopids when they move into the intergranular spaces. Such observations are documented *inter alia* in Roca and Danielopol (1991). The horizontal position of the *M. staceyi* with valves widely open and gaping at about 180°, appeared (in the laboratory at least) to be that species most common stance. This behaviour is apparent during copulation accidentally observed and recorded by K. Swanson and K. Abe (Swanson, 1996). These observations on the life style of *M. staceyi* and its very wide gape, appear to be an evolutionary solution derived from ancestors that moved with their valves gaping narrowly and aligned vertically. It represents a body plan type that displays a ventro-lateral polarity and we name it here Body plan 2a (Table 4); and is an adaption to living in an ecologically dynamic environment.

The structure and the position of the ambulatory limbs L5 to L7 of *Manawa staceyi* are considered homeomoprhic traits. These limbs are extended laterally during ambulatory activity. Their endopodites display elongated podomeres derived from the fusion of the 2nd and 3rd podomeres (ie. the merus with the carpus) and bear distally, a short claw-like dactylus. We consider the shape of the L5 – L7 an adaptive solution to the psammobiotic life, a mechanical solution with respect to both attaching to the surface of sand grains and for the penetration of intergranular spaces.

A surprising morphological similarity exists between pereiopode structures of the mesopsammic crustaceans belonging to the Isopoda Microcerberoidea, which are also psammobionts, moving through the granular spaces with thoracic limbs (pereiopodes) extended laterally, also noting that the merus and carpus of same are elongated and that the dactylus is short (Coineau, 1986 and Plesa, 1996). Therefore, it can be postulated that the origin of the special structure and functional position of the walking limbs of *Manawa staceyi,* similar to those of the thoracopodes of the isopods Microcerberoidea represent a case of homeomorphy, resulted through convergent evolution to thigmotaxis within the psammal environment. Finally, a brief observation: from the present state of our knowledge we do not have arguments to consider *Manawa staceyi* a "living fossil", a kind of relict species displaying primitive crustacean traits, as suggested by Malz (1990). In fact, the opposite is apparent, it is a species well adapted to the benthic habitats with coarse sediments and strong water currents.

4.2. The order Punciocopida Schallreuter, 1968 and the taxonomic validity of the subclass Palaeocopa Henningsmoen, 1953

In the introduction of this text, we indicated that there is wide range of views centred on the taxonomic position of the Puncioidea. Table 1 mentions at least some of those options, and we acknowledge there are others that can be added to that list. Using the taxonomic scheme of Martin and Davis (2001), and later adopted by Horne *et al.* (2002), we propose that members of the superfamily Puncioidea belong in the Order Punciocopida Schallreuter, 1968, within the Subclass Podocopa.

Schallreuter (1968) after completion of a study of Ordovician ostracod species with valves with a straight hinge and a convex ventral margin proposed a new Suborder Punciocopina with a type taxon, the genus *Puncia* (Hornibrook, 1949) and with two superfamilies, the Punciacea (in modern terms Puncioidea) and the Kirkbyoidea. However, no clear diagnosis was provided by Schallreuter (op. cit.). The current rexamination of the morphology of the limbs and the valves of *Manawa staceyi* and of the valves of *Promanawa konishii*, combined with the information already published by Hornibrook (1949) allows us now to propose such a diagnosis for the Order Punciocopida (the equivalent taxonomic level for the Suborder Punciocopina within the Martin and Davis 2001-system adopted herein).

The Order Punciocopida is characterised by quasi-symmetric valves with a straight dorsal margin and angular cardinal corners; hinge adont, ventral margin of the valves with convex marginal shape; central muscle scars located above the mid height of the valve; right valve with anterior and posterior sides of stragular process (*sensu* Swanson 1989a); outer lamella of the valves with numerous normal pores with one or two unperforated, internal plates; marginal infold developed with prominent selvage situated well inside the outer margin; inner margin denoted by a ridge located close to the selvage; vestibule and sexual dimorphism of valves observed in one taxon, *Promanawa konishii*. Diagnostic traits using the limbs and the juvenile stages presented as per *Manawa staceyi* (Swanson 1989a, 1989b): Sensorial setae emerging from normal pores of the valves placed on the outer lamella and inside on the marginal infold, the latter apparently used during assumption of venter to venter copulatory position; exopodite of the antenna elongated and with two articles and three long setae; mandibular gnathobasis of "darwinuloid" type (see above); labrum large, rectangular and flat; maxillula of the female with pediform endopodite while the equivalent morphologic character in the male transformed into a clasping organ; stenopodial limbs L5 to L7 with elongated endopodites, slightly differing in structure; an 8th limb present in front of the furca and considered homologous with the brush like organ of the Platycopida and Podocopida ostracods; copulatory complex present with only one elongated hemipenis located on the right side; a strong furca occurs anterior to the anus; posterior part of the body segmented. The three postembryonal stages with a flat dorsal shield, instead of a bivalve carapace; this latter visible first at the metanauplius M3.

The Order Punciocopida as here defined belongs to the Subclass Podocopa and displays similarities with ostracods placed in the Orders Podocopida and Platycopida.

The taxonomic relationships with the Palaeozoic kirkbyocopids are not straightforward (Becker, 1990; Becker in Becker and Swanson, 1992; Becker and Braun, 2007; Abushik, 2015). Becker (2005) as well as Becker and Braun (2007), for instance, consider as possible taxonomic placement of the Punciidae within the superfamily Drepanelloidea. This replicating the position, expressed by Becker in previous publications, in which Puncioidea were not seen as having any direct relationship to the Kirkbyoidea. Earlier taxonomic schemes such as those proposed by Hornibrook (1949), Henningsmoen (1953), Sylvester Bradley (1961) and Maddocks (1982), in which punciids were seen as having a close relationship to the beyrichicopines, have not been included in this discussion. Also the discussion in Kozur (1993) on the relationships of the punciids with other palaeocopid and podocopid groups is completely confusing. As a result, it is proposed that the Order Punciocopida should include only the superfamily Puncioidea.

Some comments with respect to a recent contribution by Yu *et al.* (2012) are also warranted. Those authors presented a phylogenetic analysis that was derived from both morphologic traits and molecular biological data, leading to their conclusion that Puncioidea, as a phylogenetic lineage, deserved the status of a Subclass, Punciocopa. However Yu *et al.* (2012) then acknowledged this as a proposal, one that needed more compeeling evidence before it could be confirmed.

The Subclass Palaeocopa, as characterised originally by Henningsmoen (1953) is probably a polyphyletic taxon, as a result, comparisons and attributions with respect to the relationship of that Subclass to Myodocopa and Podocopa is fraught at best. It is therefore legitimate to then question the taxonomic status of Palaeocopa. Does it for instance, fulfil morphologic criteria necessary for it to qualify as monophyletic group? If the answer were yes, then the present authors would accept the initial proposal of Henningsmoen (1953) resulting in Palaeocopa being given the same hierarchic status as Podocopa, namely both are Subclasses. However, as documented herein, within the Palaeocopa we find punciids belonging to Podocopa and in the same time palaeocope-like (in terms of shell morphology) species belonging to Myodocopa were also recorded (Siveter *et al.*, 2012). This situation, leading to the logical conclusion that Palaeocopa is a polyphyletic group as noted above. An alternative solution is those adopted by Vannier *et al.* (1989) giving to the palaeocopes the taxonomic rank of a suborder and a more restricted definition. Therefore, it becomes necessary to revise the taxonomy position of this rich Palaeozoic group within a more complete framework of the Class Ostracoda where both living and fossil taxa are considered. A seminal contribution to this conundrum will be offered by the potential discovery of limb-bearing Palaeozoic specimens of groups such as the kirkbyocopids.

We close this discussion offering in the figure 20 our view on the place of the Order Punciocopida, restricted to the superfamily Puncioidea, as belonging to the Subclass Podocopa.

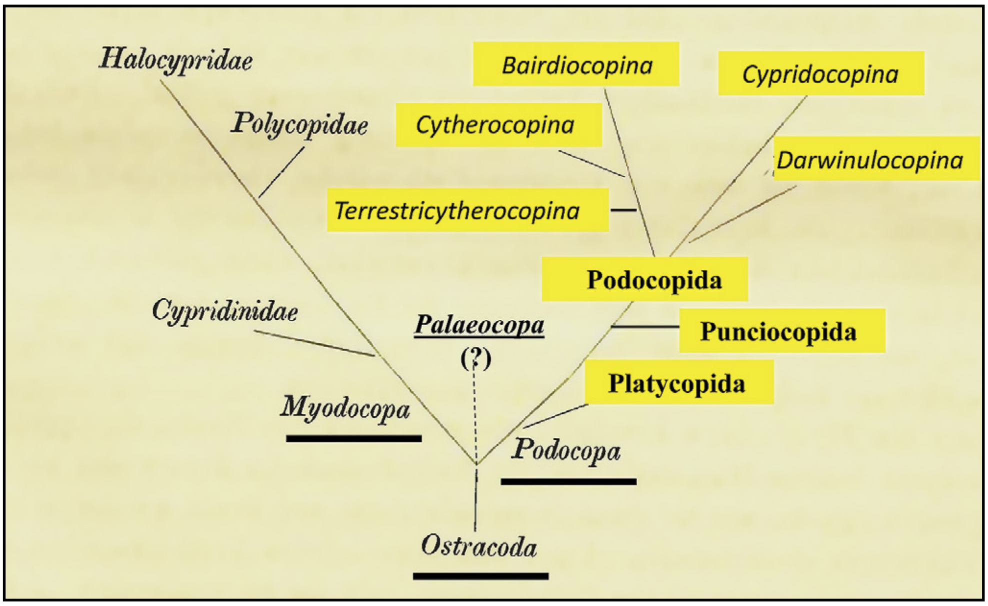


Figure 20. Revised version of the phylogenetic tree for Recent Ostracoda groups from G.W. Müller, 1894, modified as indicated in this text.

Figure 21. a-c – Sequence of the predatory reaction of *Heterocypris incongruens* before and after injuring a midge larva (*Chironomus plumosus*) (Images extracted from the videoclip of Danielopol *et al.*, 2019).

4.3. The modest species richness of Puncioidea – proposal for a non-trivial explanation

The low species richness of the superfamily Puncioidea with representatives existing other a wide area, from both Southern and Northern hemispheres (Table 2), in the context of the general pattern of the marine ostracod benthic radiations (Horne, 2003), is surprising. The record of representatives of this group over a long period of time, from the Lower Norian, Upper Triassic, i.e. about 210Mya (Kozur, 1998) to present day, invites some potential explanation. Acknowledging that the habit and life cycle of punciids remain poorly understood. Such a similar situation existed with the thaumatocyprids when these were discovered in anchialine caves (Danielopol, 1972). Since then a dozen species have been discovered in marine caves in the Atlantic, Pacific and the Indian Oceans (Danielopol *et al.*, 2000; Humphreys *et al.*, 2009). However even for areas where ostracods have been relatively-well investigated such as the coast of Japan, New Zealand and Australia, punciids were, and remain rare. Acknowledging that one contributing factor might be that that animals and especially the valves are rapidly destroyed in marine habitats with strong currents and unstable abrasive sandy sediments.

We propose here an alternative possibility derived from the assumption that the punciids actively search for their optimal environment, which once achieved, leads to the establishment of a viable and stable population. In other words punciids actively construct their own niche. Such an active exploration of the environment with a constant search for energetic resources or congeners has been documented in many non-marine ostracods, especially those belonging to the superfamily Cypridoidea. Danielopol *et al.* (2019) recorded using video-techniques, the constant movements of a groundwater dwelling ostracod, *Cryptocandona kieferi* Klie and those of a surface water dwelling, *Heterocypris incongruens* Ramdohr. For the former species, extremely long time spent in search of food, an adaptive behaviour for animals living in the oligotrophic environment of subterranean waters. The movement of the latter species in video, demonstrates their predatory life-style involves active chemical perception of their surroundings. Figure 21, a-c, presents a succession of the *Heterocypris incongruens* movements and the way the crustaceans aggregate on the midge prey (*Chironomus plumosus* L.). Similar observations, namely the demonstration of the active search as movement of ostracods can be seen also in the video-clips of Robin J. Smith placed on the home page of the Biwa laboratory (Smith, 2019).

The difference between the punciids and cypridoids is most obvious in their sensorial morphological equipment. The antennary equipment of the *Manawa staceyi* is devoid of aesthetascs, chemosesorial organs (Fig. 16b) while those of cypridoids, such as the antennae of *Candona sanociensis* Sywula (Fig. 17a-h and 18a-b), present five different types of aesthetascs, with additional sensorial setae "t" of the male being used for communication with the female during the mating process (Danielopol, 1978; Horne *et al.*, 1998). Both *Candona* and *Heterocypris* are known as genera with a high number of species (Meisch *et al.*, 2019).

Additionally, it should be noted that ostracod groups which move actively in their environment (crawling or swimming as is the case for most of the Cypridoidea), are also species rich. *Manawa staceyi* as mentioned above

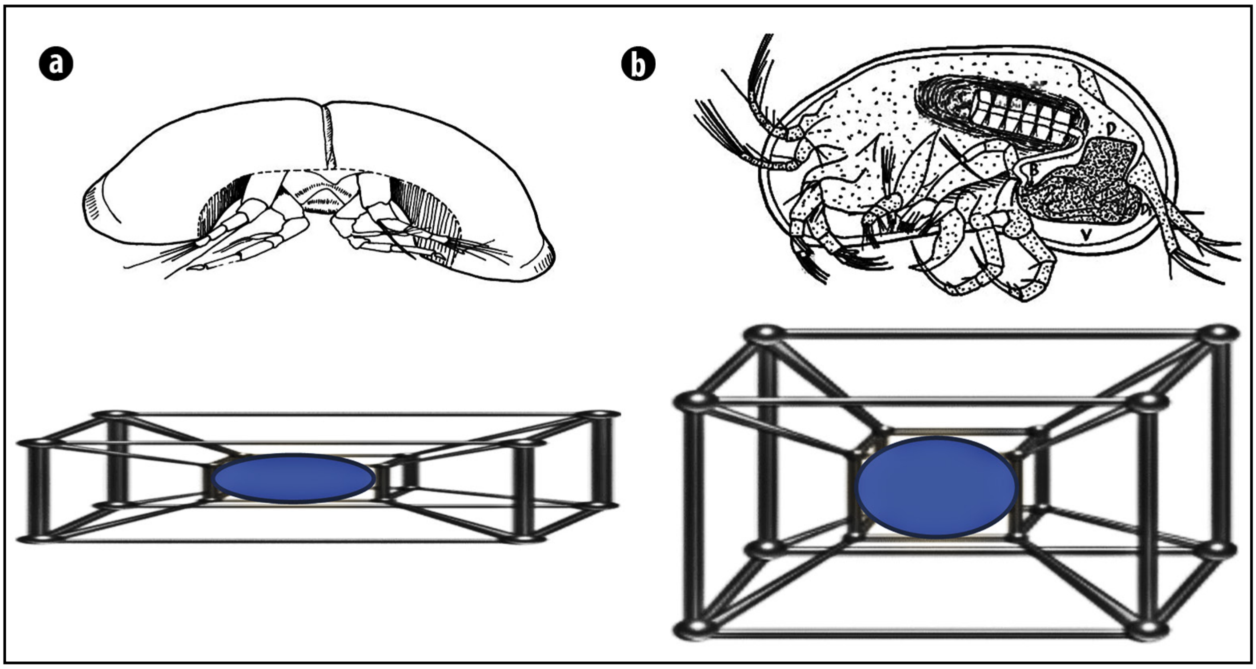


Figure 22. Virtual model using 4-D hypercube representations for the ways ostracods possibly perceive their surrounding environment: **a** – *Manawa staceyi*, "Flatland" type; **b** – *Candona neglecta*, "Spaceland" type (additional explanation, see text) (graphics Danielopol).

moves slowly on /in the sandy substrate. Finally, one has to mention that Swanson (1989b) postulated that juveniles of *M. staceyi* having flat and very light valves could disperse by floating in the marine waters. This would explain the wide biogeographic distribution of the punciids mentioned above. However Boeckner *et al.* (2009) demonstrated experimentally that meiofauna which is able to disperse through the column of water over large distances is represented mainly by animals which are able actively to leave their benthic substrate. Apparently this is not the case of *M. staceyi* which has a morphology typical for psammobiotic animals as previously documented. Hhowever, KMS has noted that in this regard *Puncia,* the other 'extant' punciid found in New Zealand waters, remains enigmatic. Valves of this frilled species are recovered (even more rarely than specimens of *Manawa*) from equivalent environments, but juveniles of same size have never been found by him. This leading to a speculative suggestion that perhaps within the punciids, a planktic lifestyle has developed in adults, this then accounting for the hemispheric distribution of same.

There is an obvious contrast in the sensorial chaetotaxic equipment and the way that punciids and the non-marine cypridoids possibly define their environmental space. The punciids, such as the psammobiotic *M. staceyi,* seem to perceive the surrounding space within a flat, quasi two dimension system (Fig. 22a). The cypridoids (Fig. 22b), on the other hand, as a result of their movement and well developed chemo-sensorial organs perceive the aquatic environment within a higher dimensional space, named by Poincaré (1902/1968) "representative space". The two groups, each with different perceptive capacities will be named, Flatlanders and Spacelanders. These are metaphoric names used already by Turvey (2019) for similar functional groups and were derived from the Abbott's fiction tale "Flatland, a romance of many dimensions" (Abbott, 1884/ 2013).

5. CONCLUSION: NEW PERSPECTIVES FROM THE REINVESTIGATION OF MORPHOLOGICAL TRAITS OF MANAWA STACEYI AND ITS RELATED TAXA.

The concluding remarks presented below are based on the assumption that the morphological traits of *Manawa staceyi* are representative for the Puncioidea, as a whole, that now raised to the status of an Order, the Punciocopida:

1. The body plan of Puncioidea tracks that pattern exhibited by Podocopa, namely it displays a ventral polarity with specific characteristics, the presence of lateral extension of the limbs during their ambulatory and feeding activities and a wide-gape, horizontal extension of the valves. In our opinion this is not a primitive state for Ostracoda but rather a derived one, with an extended geological record. This assertion should be further examined using new information.
2. The re-examination of the morphology of the limbs of *Manawa staceyi* then allows the punciids to be considered taxonomically, as an Order, the Punciocopida, within the Subclass Podocopa. This taxon proposed initially by Schallreuter (1968) receives here an enlarged diagnosis based mainly on limb traits. We propose to restrict the content of the Order Punciocopida to the ostracods belonging to the superfamily Puncioidea. The exact phylogenetic relationships between the Palaeozoic kirkbyocopines, and the post-Palaeozoic punciids, have to be re-evaluated.
3. The status of the Subclass Palaeocopa as defined by Henningsmoen (1953) can only be resolved more accurately after studies of new possible finds of limb-bearing material of, for example, kirkbyocopines and similar taxa.
4. We assume that the morphologic pattern of the horizontal position of the valves and limbs during the life activity, as observed in *Manawa staceyi* is not a primitive organismal state, but one derived from an ostracod with sagittal position of the body, with a narrow gape of the open valves, with bilateral position of the limbs (especially the male copulatory complex), with antennal and thoracic legs without morphologic transformation of the distal phanerae for substrate fixation. The peculiar aspects of the morphology of *Manawa staceyi* are considered adaptations to the special dynamic aquatic environment in which those ostracods live, coarse-grained sediments in which their habitat is dominated by grain surface and inter-granular spaces. Therefore, we consider it necessary to reinvestigate the problem of homeomorphic traits as convergent adaptive solutions adopted by different benthic ostracods groups.
5. The pediform shape of the maxillulary endopodite is interpreted as an expression of a deep homology process, the result of parallel evolution within the Podocopa. We have noted equivalent situations, also requiring further investigation and data.
6. As a non-trivial hypothesis, we propose that the reduced capacity of niche construction of punciids (viz. the obvious reduced sensorial capacity for explorative perception and activity, as compared to the non-marine Cypridoidea), is an important constraining factor for the evolutionary diversification of this group. Most probably other factors contribute to the biological rarity problem of punciocopids too. For instance the low evolvability aspect as we perceive it from the restricted taxonomic diversity. Therefore, additional investigations related to this topic are needed.
7. Finally, we suggest as a realistic perspective for the next period of scientific investigations on Ostracoda, that such effort should concentrate on a detailed examination of the morphology of those Palaeozoic ostracod groups which possess apparent phylogenetic affinities to the Punciocopida, the resultant data then being applied using the approaches discussed and/or illustrated here.

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REFERENCES

Abbott, E.A. (1884/2013). *Flatland: A romance of many dimensions*. http://www.gutenberg.org/2/0/201/201-h.htm (released 01.11.2013).

Abe, K., Vannier, J.M.C. (1993). The role of 5th limbs in mating behaviour of two marine podocopid ostracods, *Bicornucythere bisanensis* (Okubo 1 975) and *Xestoleberis hanaii* Ishizaki 1968. *In*: McKenzie, K.G. and Jones, P.J. (Eds.) *Ostracoda in the Earth and Life Sciences*: 581-590, A.A. Balkema, Rotterdam.

Abushik, A.F. (2015). Ostracods (Crustacea): Some problems of systematics. *Paleont. J.,* **49**: 485–495.

Adamczak, F. (1969). On the question of whether the Palaeocope ostracods were filter-feeders. In: J. W. Neale (Ed.) *The taxonomy, morphology and ecology of Recent Ostracoda*: 93-98, Oliver & Boyd, Edinburgh.

Arthur, W. (1997). *The origin of body plans*. Cambridge Univ. Press, Cambridge, 360pp.

Becker, G. (1990). Zur Morphologie und Taxonomie paläozoischer Ostracoda. Mit kritischen Bemerkungen zur Wertigkeit von Carapax-Merkmalen. *Senckenbergiana lethaea*, **70**: 147-169.

Becker, G. (2005). Functional morphology of Palaeozoic ostracods: phylogenetic implications. *In*: N. Ikeya, N., Tsukagoshi, A. and Horne, D.J. (Eds.) *Evolution and Diversity of Ostracoda*. *Hydrobiologia*, **538**: 23–53.

Becker, G., Braun, W.K. (2007). Extra-lobal and complex dimorphic features in Middle Devonian palaeocopine ostracods. *Hydrobiologia*, **585**: 141–157.

Becker, G., Swanson, K.M. (1992). Are the Kirkbyacea extinct palaeocopine ostracods or close relatives of the extant Punciacea? *Senckenbergiana lethaea*, **72**: 121-128.

Benson, R.H. (1965). Morphologic stability in Ostracoda. *In*: F. M. Swain (Ed.) *Biology and paleobiology of Ostracoda, Bull. Amer. Paleont*., **65**: 13-46.

Betts, M.J., Brock, G.A, Paterson, J.R. (2015). Butterflies of the Cambrian benthos? Shield position in bradoriid arthropods. *Lethaia*, DOI: 10.1111/let.12160.

Boeckner, M.J., Sharma, J., Proctor, H.C. (2009). Revisiting the meiofauna paradox: dispersal and colonization of nematodes and other meiofaunal organisms in low- and high-energy environments. *Hydrobiologia*, **624**: 91–106.

Brandão, S.N., Angel, M.V., Karanovic, I., Perrier, V., Meidla, T. (2019). *World Ostracoda Database. Puncioidea Hornibrook, 1949*. Accessed through *World Register of Marine Species* at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=715600 (11.25.2019).

Cannon, H.G. (1926). On the feeding mechanisms of a freshwater ostracod *Pionocypris vidua* (O.F. Müller). *J. Linn. Soc. London (Zool.),* **36**: 325-335.

Cohen, A.C., Martin, J.W., Kornicker, L.S. (1998). Homology of Holocene ostracode biramous appendages with those of other crustaceans: the protopod, epipod, exopod and endopod. *Lethaia,* **31**: 251-265.

Coineau, N. (1986). Isopoda; Microcerberidae. *In*: L. Botosaneanu (Ed.) *Stygofauna Mundi*, Brill Publ.: 473-479, Leiden.

Danielopol, D.L. (1968). *Microdarwinula* n.g. et quelques remarques sur la répartition de la famille des Darwinulidae Br. & Norm. (Crustacea, Ostracoda). *Annls. Limnol*., **4**: 153-174.

Danielopol, D.L. (1969). Recherches sur la morphologie de l'organe copulateur mâle chez quelques Ostracodes du genre *Candona* (Fam. Cyprididae Baird). *In*: J.W. Neale (Ed.) *The taxonomy, morphology and ecology of Recent Ostracoda*: 135-153, Olliver & Boyd, Edinburg.

Danielopol, D.L. (1970a). Sur la morphologie, l'origine et la répartition du genre *Cordocythere* Dan. (Ostracoda, Cytheridae). *In*: T. Orghidan (Ed.) *Livre du Centenaire „Emile Racovitza"*: 287-300, Edit. Academiei R.S.R., Bucuresti.

Danielopol, D.L. (1970b). Sur une nouvelle espèce du genre *Darwinula* Br. & Rob. des eaux souterraines de Roumanie et quelques remarques sur la morphologie des Darwinulidae (Ostracoda, Podocopidae). *Trav. Inst. Spéol. „Emile Racovitza",* **9**: 135-149.

Danielopol, D.L. (1971). Définition de la tribu des Hartiellini et remarques sur la poécilogynie de *Hartiella dudichi* (Ostracoda, Entocytheridae, Sphaeromicolinae). *Trav. Inst. Spéol. „Emile Racovitza"*, **10**: 189-207.

Danielopol, D.L. (1972). Sur la présence de *Thaumatocypris orghidani* n.sp. (Ostracoda, Myodocopida) dans une grotte de Cuba. *C.R. Acad. Sc. Paris*, (Série **D**), **274**: 1390-1393.

Danielopol, D.L. (1973). Sur la morphologie des aesthetascs chez quelques Ostracodes hypogés de la sous- famille des Candoninae (Cyprididae, Podocopida). *Ann. Spéléol.*, **28**: 233-245.

Danielopol, D.L. (1976). Supplementary data on *Pusella botosaneanui* Dan. (Ostracoda, Bairdiidae). *Vie Milieu*, **26** (*2A*): 261-273.

Danielopol, D.L. (1978). Über Herkunft und Morphologie der süßwasserhypogäischen Candoninae (Crustacea, Ostracoda). *Sitz. Ber. Österr. Akad. Wiss., Math.-Nat. Kl. Abt.* **I** (*187*): 1-162.

Danielopol, D.L. (1980). Sur la biologie de quelques Ostracodes Candoninae épigés et hypogés d'Europe. *Bull. Mus. Natn. Hist. nat., Paris*, **4**e sér., **2**, sect. **A, 2**: 471-506.

Danielopol, D.L., Martens, K., Casale, L. (1989). Revision of the genus *Leucocythere* Kaufmann, 1892 (Crustacea, Ostracoda, Limnocytheridae), with the description of a new species and two new tribes. *Bull. Inst. Roy. Sci. Nat. Belg. Biol.,* **59**: 63-94.

Danielopol, D.L., Casale, L., Rogulj, Strobl, J., Maier, K. (1990). Spatial distribution of *Cytherissa lacustris* living in Mondsee. In: Danielopol, D.L., Carbonel, P. & Colin, J.-P. (Eds.), *Cytherissa (Ostracoda), the Drosophila of Paleolimnology. (Scientific results of a multidisciplinary project on recent and fossil Ostracoda). Bull. Inst. Géol. Bassin Aquitaine*, **47-48**: 139-165.

Danielopol, D.L., Baltanás, A., Humphreys, W.F. (2000). *Danielopolina kornickeri* n.sp. (Ostracoda, Thaumatocyprididae) from a Western Australian anchialine cave: morphology and evolution. *Zool. Scr.*, **29**: 1-16.

Danielopol, D.L., Cabral, C.M., Lord, A., Carbonel, P., Gross, M., Stoica, M., Humphreys, W.F., Namiotko, T., Tóth, E., Külköylüoğlu, O., Piller, W.E., Nuněs, T. (2018). Sieve-type pore canals in the Timiriaseviinae. A contribution to the comparative morphology and the systematics of the Limnocytheridae (Ostracoda, Crustacea). *Zootaxa,* **4495** (*1*): 1–64.

Danielopol, D.L., Benassi, G., Baltanás, A. (2019). *Niche construction of two non-marine ostracods.* Video: iewarchiv.uni-graz.at/ zusatzmaterial/

Dupré, J. (2001). In defence of classification. *Stud. Hist. Phil. Biol. & Biomed. Sci.*, **32**: 203–219.

Ereshefsky, M. (1989). Species, higher taxa, and the units of evolution. *Phil. Sci.*, **58**: 84-101.

Foote, M., Sepkosky, J.J. (1999). Absolute measures of the completeness of the fossil record. *Nature*, **398**: 415-417.

Giere, O. (1993). *Meiobenthology – The Microscopic Fauna in Aquatic Sediments*, Springer Verlg., Heidelberg, 328pp.

Hanai, T., Tabuki, R. (1995). Shell structure of *Promanawa* – Discussion on the Bauplan of podocopid Ostracoda. *Mitt.hamb.zool.Mus. Inst.,* **92**: 259 – 272.

Harding, J.P. (1964). Crustacean cuticle with reference to the ostracod carapace. *Publ. staz. zool. Napoli,* Suppl. **33**: 9-31.

Hartmann, G. (1966, 1967, 1968, 1975, 1989). Ostracoda. *In*: Bronns H. G. (Ed.) *Klassen und Ordnungen des Tierreiches*, Bd. 5, Abt. 1, Buch 2, Teil 4, Lief. 1-5, Gustav Fischer Verlg.:1-1067, Jena.

Hartmann, G. (1973). Zum gegenwaertigen Stand der Erforschung der Ostracoden interstitieller Systeme. *Ann. Spéleol.,* **28**: 417-426.

Hartmann, G. (1978). Teil 1. Die Ostracoden der Ordnung Podocopida G. W. Müller, 1894 der tropisch-subtropischen Westküste Australiens (zwischen Derby im Norden und Penh im Süden). *In*: Hartmann-Schröder, G. and Hartmann, G. – Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitt. hamb. zool. Mus. Inst.,* **75**: 64 -219.

Henningsmoen, G. (1953). Classification of Paleozoic straight-hinged ostracods. *Norsk Geol. Tidsskrift*, **31**: 185-288.

Herrig, E. (1988). Punciide Ostrakoden aus der höheren Oberkreide der Mittleren Ostsee. *Mitt. Gesellschaft Geschiebekunde*., **4**: 33-37.

Herrig, E. (1991). Neue Ostrakoden aus verkieselten Kalksteinen der höheren Oberkreide (Ober-Maastricht) der Dänisch-Polnischen FurchelOstsee., *Geol. Jb.* **A1** (*28*): 99-115.

Hinz-Schallreuter, I., Schallreuter, R. (1999). *Ostrakoden*. Enke Verlg., Stuttgart, 168 pp.

Horne, D.J. (2003). Key events in the ecological radiation of Ostracoda *In*: Park, L.E. and Smith, A.J. (Eds.) *Bridging the Gap: Trends in the Ostracode Biological and Geological Sciences. The Paleontological Society Papers*, **9**: 181-201.

Horne, D.J., Danielopol, D.L., Martens, K. (1998). Reproductive behaviour. *In*: Martens, K. (Ed.) *Sex and parthenogenesis. Evolutionary ecology of reproductive modes in non-marine ostracods*: 157-195, Backhuis, Leiden.

Horne, D.J., Cohen, A., Martens, K. (2002). Taxonomy, morphology and biology of Quaternary and living Ostracoda. In: Holmes, J.A. and Chivas, A.R. (Eds.) *The Ostracoda, applications in Quaternary research. Geophys. Monogr*., **31**: 5-36, American Geophys. Union, Washington, DC.

Horne, D.J., Smith, R.J., Whittaker, J.E., Murray, J.W. (2004). The first British record and a new species of the superfamily Terrestricytheroidea (Crustacea, Ostracoda): morphology, ontogeny, lifestyle and phylogeny. *Zool. J. Linn. Soc.*, **142**: 253–288.

Horne, D.J., Schön I, Smith R.J., Martens. K. (2005). What are Ostracoda? A cladistic analysis of the extant superfamilies of the Subclasses Myodocopa and Podocopa (Crustacea: Ostracoda). *In*: Koenemann, S. and Jenner, R.A. (Eds.) *Crustacea and Arthropod Relationships*: 249-272, CRC Press, Boca Raton.

Hornibrook, N. de B. (1949). A new family of living Ostracoda with striking resemblances to some Palaeozoic Beyrichiidae. *Trans. Roy. Soc. N. Z.*, **71**: 469-47l.

Hornibrook, N. de B. (1963). The New Zealand ostracode family Punciidae. *Micropaleontology*, **9**: 318-320.

Hou, X., Williams, M., Siveter, Da.J., Siveter, De.J., Aldridge, D.J. , Sansom, R.S. (2010). Soft-part anatomy of the Early Cambrian bivalved arthropods *Kunyangella* and *Kunmingella*: significance for the phylogenetic relationships of Bradoriida. *Proc. R. Soc. B.*, **277**: 1835-1841.

Humphreys, W.F., Kornicker, L.S., Danielopol, D.L. (2009). On the origin of *Danielopolina baltanasi* sp. n. (Ostracoda, Thaumatocypridoidea) from three anchialine caves on Christmas Island, a seamount in the Indian Ocean. *Crustaceana*, **82**: 1177-1203.

Hutchinson, E.G. (1957). Concluding remarks. *Cold Spring Harbor Symposia. Quantitative Biology*, **22**: 415-427.

Ishizaki, K. (1973). Discovery of the family Punciidae, Ostracoda (Crustacea) from Okinawa Island, Japan. *Sci. Repts. Tohoku Univ.,* 2nd Ser., **6**: 403-405.

Iwatani, H., Irizuki, T., Yashuhara, M. (2013). Occurrence of a rare puncioid ostracod, *Promanawa konishii* (Nohara, 1976), in Recent sediments of the East China Sea. *J. Micropal.*, **32**: 221-223.

Jaanusson, V. (1985). Functional morphology of the shell in platycope ostracodes – a study of arrested evolution. *Lethaia*, **18**: 73-84.

Jeannel, R. (1950). *La marche de l'évolution*. Presses Univ. France, Paris, 171pp..

Klingenberg, C.P. (2008). Morphological integration and developmental modularity. *Ann. Rev. Ecol. Evol. Syst.*, **39**: 115-132.

Kozur, H. (1972). Einige Bemerkungen zur Systematik der Ostracoden und Beschreibung neuer Platycopida aus der Trias Ungarns und der Slowakei. *Geol. Paläont. Mitt. Innsbruck*, **2**: 1-27.

Kozur, H. (1993). Relation between Late Paleozoic-Triassic Kirkbyacea and Cretaceous-Recent Punciacea (Ostracoda). *In*: McKenzie, K.G. and Jones, P.J. (Eds.) *Ostracoda in the earth and life sciences*: 91-106, A.A. Balkema. Rotterdam.

Kozur, H. (1998). Upper Triassic Punciacea, the connecting link between the Palaeozoic to Lower Triassic Kirkbyacea and the Cretaceous to Cenozoic Punciacea. *Bull. Centre Rech. Elf. Explor. Prod.*, Mém. **20**: 257-267.

Laland, K., Uller, T., Feldman, M., Sterelny, K., Müller, G.B., Moczek, A., Jablonska, E., Odling-Smee, J., Wray, G.A., Hoekstra, H.E., Futuyma, D.J., Lenski, R.L., Mackay, T.F.C. (2014). Does evolutionary theory need a rethink? *Nature*, **514**: 161-164.

Lewontin R. (1985). The organism as subject and object of evolution. In: Levins, R. and Lewontin R.– *The dialectical biologist*: 85-106, Harvard Univ. Press, Cambridge MA.

Lewontin R.C. (2001). Foreword. In: Wagner, G.P. (Ed.) *The character concept in evolutionary biology*: XII-XXIII, Academic Press, San Diego.

Liebau, A. (2005). A revised classification of the higher taxa of the Ostracoda (Crustacea). *In*: N. Ikeya, N., Tsukagoshi, A. and Horne, D.J. (Eds.) *Evolution and Diversity of Ostracoda. Hydrobiologia,* **538**: 115–137.

Lord, A.R., Cabral, M., Danielopol, D.L. (2019). Sieve-type normal pore canals in Jurassic ostracods. a review with description of a new genus. *Acta. Palaeont. Polonica* (*in press*).

Maas, A., Waloszek, D., Müller, K.J. (2003). Morphology, ontogeny and phylogeny of the Phosphatocopina (Crustacea) from the Upper Cambrian "Orsten" of Sweden. *Fossils and Strata*, **49**: 1-238.

Maddocks, R.F. (1976). Pussellidae are interstitial Bairdiidae (Ostracoda). *Micropaleontology*, **22**: 194-214.

Maddocks, R.F. (1982). Ostracoda. *In*: Abele, L.G. (Ed.) *The biology of Crustacea; 1, systematics, the fossil record and biogeography,* Academic Press: 221-239, New York.

Maddocks, R.F. (1990). Living and Fossil Macrocyprididae (Ostracoda). *The university of Kansas, Paleontological Contributions, Monograph* **2**: 1-189.

Malz, H. (1990). Bericht über das "1st European Ostracodologists' Meeting im Senckenberg Museum (2.-8. August 1989). *Natur und Museum*, **120**: 19-21.

Martens, K. (1990). Revision of African *Limnocythere* s. s. BRADY, 1867 (Crustacea, Ostracoda), with special reference to the Rift Valley Lakes: morphology, taxonomy, evolution and (palaeo-) ecology. *Arch. Hydrobiol*. Suppl. **83** (*4*): 453-524.

Martin, J.W., Davis, G.E. (2001). An updated classification of the recent Crustacea. *Natural History Museum of Los Angeles County. Contrib. Sci.* N° **39**: 1-124.

McKenzie, K.G., Neil, J.V. (1983). *Promanawa* gen. nov., an Australian Miocene punciid ostracode from Hamilton, Victoria. *Proc. R. Soc. Victoria,* **95**: 59-64.

Meisch C., Smith, R.J., Martens, K. (2019). A subjective global checklist of the extant non-marine Ostracoda (Crustacea). *Europ. J. Taxonomy,* **492**: 1–135.

Müller, G.W. (1894). Die Ostracoden des Golfes von Neapel und der angrenzenden Meeresabschnitte. In: Zoologisches Station zu Neapel (Ed.), *Fauna und Flora des Golfes von Neapel und der angrenzenden Meeresabschnitte. Monogr.*, **21**: 1-404. Friedländer & Sohn, Berlin.

Newman, W.A. (2005). Origin of the Ostracoda and their maxillopodan and hexapodan affinities. *In*: Ikeya, N. Tsukagoshi, A. and Horne, D.J. (Eds.) *Evolution and Diversity of Ostracoda. Hydrobiologia,* **538**: 1–21.

Nohara, T. (1976), Ostracod of the genus *Manawa* from Pleistocene Chinen sands of Okinawa-jima. *Geol. Stud. Ryukyu Isls.*, **1**: 75-78.

Nohara, T., Nakasone, N. (1982). Sexual dimorphism of the paleocopid ostracode genus *Manawa* from Okinawa-Jima *Trans. Proc. Paleontol. Soc. Japan*, N.S., **127**: 364-367.

O'Hara, R.J. (1997). Population thinking and tree thinking in systematics. *Zool. Scr.,* **26**: 323-329.

Oakley, T.H., Wolfe, J.M., Lindgren, A.R., Zaharoff, A.K. (2012) – Phylotranscriptomics to bring the understudied into the fold: monophyletic Ostracoda, fossil placement, and pancrustacean phylogeny. *Mol. Biol. Evol.*, **30**: 215–233.

Odling-Smee, J.F., Laland, K.N., Feldman, M.W. (2003). *Niche construction. The neglected process in evolution*. Princeton U.P., Princeton, 472 p.

Okada, R., Tsukagoshi, A., Smith, R.J., Horne, D.J. (2008). The ontogeny of the platycopid *Keijcyoidea infralittoralis* (Ostracoda: Podocopa). *Zool. J. Linn. Soc.*, **153**: 213–237.

Plesa, C. (1996). Sur un remarquable cas d'adaptation à la vie dans l'interstitiel (Psammal): *Microcerberus plesai* Chappuis et Delamare Deboutteville (Crustacea, Isopoda, Microcerberidae). *Mém. Biospéol.,* **23***:* 87-89.

Poincaré, H. (1902/1968). *La science et l'hypothèse*. Flammarion, Paris, 252 p.

Queiroz de, K. (1999). The general lineage concept of species and the defining properties of the species category. *In*: R.A. Wilson (Ed.) *Species, new interdisciplinary essays*: 49-89, Bradford/MIT Press, Cambridge MA.

Racovitza, E.G. (1926). L'Institut de Spéologie de Cluj. VI. Biospéologica, idées directrices, programme, état de la publication. *Trav. Inst. Spéologie Cluj*, **1**: 1–50.

Roca, J., Danielopol, D.L. (1991). Exploration of interstitial habitats by the phytophilous ostracod *Cypridpopsis vidua* (O.F. Müller): experimental evidence. *Annls. Limnol*. **27**: 243-252.

Rosenzweig, M.L. (1987). Habitat selection as a source of biological diversity. *Evol.Ecol*., **1**: 315-330.

Rouch, R., Danielopol, D.L. (1999). Active dispersal of *Stenasellus virei boui* Magniez (Isopoda) through alluvial sediments of a Pyrenean stream (Southern France). *Crustaceana*, **72**: 849-862.

Sars, G.O. (1866). Oversigt af Norges marine Ostracoden. *Nor. Vidensk.-Akad., Forh.*: 1-130., Christiania.

Sars, G.O. (1923). *An Account of the Crustacea of Norway*, **9**, *Ostracoda*, Parts **3-4**: 33 -77, Bergen Museum, Bergen.

Schallreuter, R. (1968). Ordovizische Ostracoden mit geradem Schlossrand und konkaven Ventralrand. *Wiss. Z. Ernst-Moritz-Arndt-Univ. Greifsw., Math.-Naturwiss. Reihe,* **17**: 127-152.

Schram, F.R. (2013). Comments on crustacean biodiversity and disparity of body plans. In: Watling, L. and Thiel, M. (Eds.) *Functional morphology and diversity*: 1-33, Oxford Univ. Press, New York.

Serban, E. (1972). *Bathynella* (Podophallocarida : Bathynellacea). *Trav. Inst. Spéol. «Émile Racovitza»*, **11**: 11–226.

Shubin, N., Tabin, C., Caroll, S. (1997). Fossils, genes and the evolution of animal limbs. *Nature*, **388**: 639-648.

Shubin, N., Tabin, C., Caroll, S. (2009). Deep homology and the origins of evolutionary novelty. *Nature*, **457**: 818-823.

Siveter, Da.J. (2008). Ostracods in the Palaezoic? *Senckenbergiana lethaea*, **88**: 1-9.

Siveter, Da.J., Briggs, D.E.G., Siveter, De.J., Sutton, M.D., Joomun, S.C. (2012). A Silurian myodocope with preserved soft-parts: cautioning the interpretation of the shell-based ostracod record. *Proc R Soc B,* **280**: 20122664, 1-6.

Siveter, Da.J., Tanaka, G., Farrell, C.Ú., Martin, M.J., Siveter, De. J., Briggs, D.E.G. (2014). Exceptionally preserved 450 million-year-old Ordovician ostracods with brood care. *Curr. Biol.,* **24**: 801-806.

Smith, R.N. (1965). Musculature and muscle scars of *Chlamydotheca arcuata* (Sars) and *Cypridopsis vidua* (O.F. Müller) Ostracoda Cyprididae. In: Kesling, R.V., Darby, D.V., Smith, R.N. and Hall, D.D. (Eds.) *Four Reports of ostracod investigations*: 1-40, *Univ Michigan, NSF-Project GB*-**26**.

Smith, R.J. (2000). The morphology of the upper lip of Cypridoidea ostracods; taxonomic and phylogenetic significance. *Hydrobiologia,* **418:** 169–184.

Smith, R.J. (2019). Freshwater ostracods, *Heterocypris incongruens*. https://www.biwahaku.jp./smith/photos.html (accessed 28.11.2019).

Smith, R.J., Kamiya, T. (2005). The ontogeny of the entocytherid ostracod *Uncinocythere occidentalis* (Kozloff & Whitman, 1954) Hart, 1962 (Crustacea). *In*: Ikeya, N.,Tsukagoshi, A. and Horne, D.J. (Eds.), *Evolution and Diversity of Ostracoda*, *Hydrobiologia,* **538**: 217–229.

Smith, R.J., Kamiya, T. (2008). The ontogeny of two species of Darwinuloidea (Ostracoda, Crustacea). *Zool.Anz.,* **247**: 275–302.

Swanson, K.M. (1985). The discovery of living punciid ostracodes in New Zealand. *New Zealand Geol. Survey Record,* **9**: 87-89.

Swanson, K.M. (1989a). Ostracod Phylogeny and Evolution – a manawan perspective. *Cour. Forsch.-Inst. Senckenberg,* **113**: 11-20.

Swanson, K.M. (1989b). *Manawa staceyi* n. sp. (Punciidae, Ostracoda): soft anatomy and ontogeny. *Cour. Forsch.-Inst. Senckenberg,* **113**: 235-249.

Swanson, K.M. (1990). The punciid ostracod: a new crustacean evolutionary window. *Cour. Forsch.-Inst. Senckenberg,* **123**: 11-18.

Swanson, K.M. (1991). Distribution, affinities and origin of the Punciidae (Crustacea, Ostracoda). *Mem. Queensland Mus*., **31**: 77-92.

Swanson, K.M. (1993). The cythereline hemipenis and the evolution of platycope ostracods. In: McKenzie, K.G. and Jones, P.J. (Eds.) *Ostracoda in the earth and life sciences*: 591-598, A.A. Balkema. Rotterdam.

Swanson, K.M. (1996). Marine benthic ostracod ecology, taphonomy and evolution: studies from the South West Pacific. *Hokkaido University Collection of Scholarly and Academic Papers. Doctoral Thesis*: http://hdl.handle.net/2115/51352/ 298705

Swanson, K.M., Jellinek, T., Malz, H., (2005). The platycopine condition; new observations on respiration and feeding in living, deep-sea Platycopina (Crustacea, Ostracoda). *Senckenbergiana maritima*, **35**: 157-187.

Sylvester-Bradley, P.C. (1961). ?Superfamily Punciacea Hornibrook, 1949. *In*: Moore, R.C. (Ed.) *Treatise on invertebrate Paleontology,* **Q**-*Arthriopoda,* **3** *(ostracodes). Geol. Soc. America and Univ. Kansas Press*: 178-179, Lawrence.

Tabacaru, I.G., Danielopol, D.L., Juvara-Bals, I. (2018). In memory of Emil G. Racovitza (1868–1947) – His ideas reverberate in our scientific research. *Trav. Inst. Spéol. «Émile Racovitza»*, **57**: 3–33.

Tinn, O., Oakley, T.H. (2008). Erratic rates of molecular evolution and incongruence of fossil and molecular divergence time estimates in Ostracoda (Crustacea). *Mol. Phyl. Evol*., **48**: 157–167.

Tsukagoshi, A., Parker, A.R. (2000). Trunk segmentation of some podocopine lineages in Ostracoda. In: Horne, D.J. and Martens, K. (Eds.) *Evolutionary biology and ecology of Ostracoda. Hydrobiologia,* **419**: 15–30.

Tsukagoshi, A., Okada, R., Horne, D.J. (2006). Appendage homologies and the first record of eyes in platycopid ostracods, with the description of a new species of *Keijcyoidea* (Crustacea: Ostracoda) from Japan. *Hydrobiologia* **559**:255–274.

Turvey, M.T. (2019). *Lectures on perception; an ecological perspective*. Routledge, New York, 432pp.

Valentine, J.W., (1985). Fossil record of baupläne and its implications. *In*: Raup, D.M. and Jablonski, D. (Eds.) *Patterns and processes in the history of life*: 209-231, Springer Verlg, Berlin.

Vannier, J., Siveter, Da.J., Schallreuter, R. (1989). The composition and palaeogeographical significance of the Ordovician ostracode faunas of Southern Britain, Baltoscandia and Ibero-Armorica. *Palaeontology*, **32**: 163-222.

Vannier, J., Abe, K. (1995). Size, body plan and respiration in the Ostracoda. *Palaeontology*, **38**: 843-873.

Wagner, J.P. (2014). *Homology, genes and evolutionary innovation*. Princeton Univ. Press, Princeton, 478 p.

Wagner, J.P. (2016). What is "Homology Thinking" and what is it for?. *J. Exp. Zool. (Mol. Dev. Evol.),* **326B**: 3-8.

Wagner, J.P., Laubichler, M.D. (2004). Rupert Riedl and the resynthesis of evolutionary and developmental biology; body plans and evolvability. *J. Exp. Zool. (Mol. Dev. Evol.),* **302B**: 92-102.

Wagner, J.P., Pavlicev, M., Cheverud, J.M. (2007). The road to modularity. *Nature Reviews/Genetics*, **8**: 921-930.

Wakayama, N. (2007). Embryonic development clarifies polyphyly in ostracod crustaceans. *J. Zool.,* **273:** 406-413.

Whatley, R.C., Siveter, D.J., Boomer, I.D. (1993). Athropoda Crustacea (Ostracoda). *In*: Benton, M.J. (Ed.) *The fossil record 2*: 343-256, Chapman and Hall, London.

Williams, M., Siveter, D.J., Salas, M.J., Vannier, J., Popov, L.E., Pour, M.G. (2008). The earliest ostracods, the geological evidence. *Senckenbergiana lethaea*, **88**: 11-21.

Wikipedia (2019). *National Centre for the Performing Arts, China*. http:// en.m. wikipedia.org/wiki/*National_Centre_for_the _Performing_ Arts_China* (accessed 28.11.2019).

Yamada, S. (2007a). Ultrastructure of the carapace margin in the Ostracoda (Arthropoda: Crustacea). *Hydrobiologia*, **585**: 201–211.

Yamada, S. (2007b). Structure and evolution of podocopan ostracod hinges. *Biol. J. Linn. Soc.*, **92**: 41–62.

Yu, N., Li, C.E., Chen, L.Q. (2012). Combined morphological and molecular analyses of higher taxa in Ostracoda. *J. East China Norm. Univ. (Nat. Sci):* 1-12, **DOI** 10.3969/j.issn.1000-5641.

Zhai, D., Williams, M., Siveter, Da.J., Harvey, T.H.P., Sansom, R.S., Gabbott, S.E., Siveter, De.J., Ma, X., Zhou, R-Q., Liu, Y., Hou, X-G. (2019). Variation in appendages in early Cambrian bradoriids reveals a wide range of body plans in stem-euarthropods. *Comm. Biol.*, **2**: 329. doi.org/10.1038/s42003-019-0573-5